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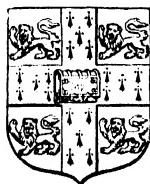
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WITH TWENTY-SEVEN PLATES, AND NUMEROUS  
FIGURES IN THE TEXT



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## FURTHER STUDIES OF THE VEGETATION ON ISLANDS IN THE INDIAN OCEAN

BY D. VESEY-FITZGERALD

(*With one Map in the Text*)

### INTRODUCTION

THE floras of the elevated granitic islands comprising the Seychelles have been described in a previous paper. The present paper deals with a further series of islands which come under the same administration. These islands form collectively those known as the Amirantes and the Aldabra Islands. The former are sand cays at present worked as coconut estates, and so their primary vegetation has been destroyed. The latter are limestone islands which still largely retain their former vegetation, and it is these which will form the subject of the present paper. In order to make the study complete, however, in addition to the Aldabra Islands proper, namely, Aldabra, Assumption, Astove and Cosmoledo, it is necessary to include the more distant islands of St Pierre and Farquhar which also belong to the limestone series.

Fryer (1910) has given a description of the geological structure of these islands, so in the present study it is only necessary to note that they are islands of coral origin which at some time in the past have become raised in relation to the surface of the sea and are at the present time in the process of being worn down. Before recording the vegetation, however, the forces acting upon these islands must be considered.

There is a very marked wet and dry season, the latter extending from March to November. The islands are not big enough to have rivers, so there is no washing of the land surface into stream channels. The islands have a very small rainfall, e.g. on Aldabra about 38 cm. (15 in.) per annum, which rapidly percolates into the ground. The precipitation has the effect, however, of etching the metamorphic limestone into a fretted surface which gives it a very rugged appearance known locally as 'champignon'. In the main the surface of the islands is level and at an elevation of about 5 m. above sea-level. Around the seaward coast the pounding of the waves eats into the land rim, breaking it down or forming overhanging cliffs. In the centre of most of the islands there is a lagoon. The shores of these lagoons are being continually dissolved away so that the lagoon surfaces are increasing and the land surfaces decreasing. Around the open coasts of the islands fragments of coral in various degrees of disintegration are deposited as shingle and sand. In places where the waves have broken down the coastal cliffs the wind is able to blow the finer coral sand up on to the island. The prevailing winds of the latitudes in which the islands are

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situated are from the south-east, and so sand dunes are built up along the exposed coasts which have an easterly or southerly aspect. Hence on most of the islands there is a peripheral coastal fringe of sea-washed detritus which may even be thrown up on to the low cliffs especially around the mouths of blow-holes, and on the windward coasts dunes are often found. The best developed dune, reaching a height of 30 m., is on Assumption Island. These dunes are characterized by a gently sloping seaward face and a steeply sloping landward face under the lee of which is a sheltered zone. Deep wind-scoured gullies divide the dunes into numerous minor ridges and valleys. In places where the cliffs are still intact and too high for sand to be thrown up in any great quantity the shore is bathed in an almost continual shower of spray.

As a result of all these forces therefore the land surface becomes secondarily raised into dunes or lowered into tide-flooded creeks and the vegetation becomes modified as a consequence. But besides these physical agents there is a very important biological agent influencing both the topography and the flora of the islands. From the remote past to the present day sea birds have nested on these islands. Years ago their numbers were very much greater than they are to-day, and as a consequence vast deposits of guano have accumulated in a semi-fossil state on parts of some of the islands. The present-day nesting birds influence the vegetation both by their deposits of fresh guano and by their trampling. But the greatest recent influence of all has been the exploitation of the guano, during which process parts of some of the islands have been cleared of vegetation.

### **PLANT COMMUNITIES**

#### *Mixed scrub*

This type of vegetation is best developed on the most elevated parts of the limestone areas of Aldabra Island, and it is also to be found in a restricted amount on parts of Cosmoledo and Assumption. It occurs on a rugged pavement of rock, the surface of which is characterized by loose flat slabs and basin-like depressions. Crevices and open pits are frequent. Some of these contain water at the bottom which is in connexion with the lagoon or the open sea. In more restricted areas the surface of the limestone is carved into the most fantastic shapes, and the numerous bosses and pinnacles resound with a metallic ring when struck. Much of the rock surface is bare, but a fine soil collects in the depressions.

The community is a mixed, partially deciduous scrub of small trees or shrubs reaching a very uneven height from place to place but averaging about 4–5 m. The density of the growth varies greatly with the nature of the topography; in parts it is impenetrable, but numerous open lanes usually allow passage in all directions. The trees have small, simple, elliptical or oval leaves. About one-third of the species are with spines.

*Sideroxylon inerme* is the most characteristic plant and is the species which extends farthest into neighbouring communities. There are about fifteen other species more or less constantly present, and these include *Elaeodendron* sp., *Gymnosporia senegalensis*, *Apodytes mauritiana*, *Erythroxylum acranthum*, *Ochna fryeri*, *Tarenna supra-axillaris*, *Flacourtie indica*, *Polysphaeria multiflora*, *Terminalia fatraea* and *Scutia myrtina*.

The present community finds its optimum conditions on the more sheltered parts of the land rim of the islands. Near exposed coasts it is replaced by a depauperated, wind-blown phase in which many of the above species are not present, but are replaced by a more maritime element. The *Sideroxylon* persists and with it are associated *Scaevola frutescens* and *Guettarda speciosa*, all of which are represented by low wind-moulded shrubs less than 1 m. high and usually with barren spaces between. Doubtless during the rains there are many herbs in this area, but these are not in evidence in the dry period except for clumps of the grass *Sclerodactylon macrostachyum*. Clumps of a *Pandanus* are occasionally a feature of this area. In some places this vegetation has been almost eliminated through the combined destruction caused by goats and fuel cutting by the turtle hunters.

It seems probable that on some of the smaller islands, as for example St Pierre, a deciduous woodland of *Pisonia grandis* and *Euphorbia abbottii* occupied a similar terrain. On such islands there were deep deposits of guano. This phase of the scrub community has, however, now been completely cut out, partly during the clearing of the land for guano extraction and partly to obtain fuel for the purpose of distilling drinking water from sea water. At the present time only relict trees remain, but early visitors to these islands recall an impassable thicket of these species.

Where the mixed scrub has been cleared prior to guano extraction a secondary mat of *Plumbago aphylla* has covered the land, and the original scrub formation is only represented by islets of shrubs chiefly around open pits. On parts where the clearing has been more frequent or where there has been trampling, the *Plumbago* has, in its turn, given place to a growth of mixed exotic weeds such as *Stachytarpheta jamaicensis*, *Dactyloctenium pilosum*, and many others.

#### Memphis thicket

This community is located on the rather lower-lying areas of metamorphic limestone, the surface of which is fretted into jagged edges by weathering agents. This is the formation locally called 'champignon', and it forms a zone along both the sea and the lagoon coasts of the islands. The former is only a narrow strip along the tops of the overhanging cliffs which rise a few feet above high-water mark. The latter is a much wider zone intersected by creeks and tidal flats, and along the windward lagoon shore isolated blocks form islets. These islets are of small area and their edges are eaten into by the action of

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the water to form overhanging cliffs. The result is that they stand up like gigantic mushrooms. Ultimately, the 'stalk' of the mushroom becomes too weak to support the block and it topples over on to its side. The rugged surface of the 'champignon' is broken up by pits at the bottom of which is a yellow mud perforated by numerous crab-holes.

The community is an impassable thicket of *Pemphis acidula* which over large tracts forms a pure stand. *Sideroxylon inerme* is, however, a fairly frequent associate, especially where mixed scrub is near. Along the sea-coast *Pemphis* forms only a narrow and broken fringe. For example, wherever sand is thrown up on to the limestone, psammophilous plants come in and, where the sea breezes are very strong, *Pemphis* is very stunted or disappears altogether.

In crossing the *Pemphis* zone at right angles to its long axis, three phases are seen. Phase 1 is that abutting on the rugged pavement which has been described above. The 'champignon' rock has a solid appearance and is perforated only by rounded holes. This type supports a *Pemphis-Sideroxylon* association. Next to this is phase 2 which lies at a slightly lower level and the surface of which is broken up into deep pits and crevices. On this grows pure *Pemphis* thicket.

Phase 3 is at a still lower level and is liable to flooding by high spring tides. Interstices between the rocks are filled with a deposit of fine lagoon sediment in which crab-holes are frequent and dead turret shells are scattered over the surface. *Pemphis* grows in such situations, but the formation is open, the bushes are stunted and, where flooding with sea water has been frequent, many of them are in a dying condition. Beyond this last zone, where the high tide regularly reaches, *Pemphis* is absent, being replaced by a carpet of extremely halophytic herbs.

#### *Mangrove communities*

Where the land surface is worn down to sea-level mangroves come in. The exposed open sea coasts are not colonized by mangroves. Hence the mangrove zone is to be found only on the more tranquil lagoon shores. It is therefore only found on the atolls and is not represented on islands such as Assumption and St Pierre.

The open lagoon floor which is left exposed by low spring tide is covered by a sediment of very fine white mud. The depth of this deposit depends on the scouring action of the tide, and this itself depends on the proximity and size of the passes to the open sea. The open tidal flats are not covered with mangroves, but up the creeks and channels, where arms of water extend into the land, mangrove forests grow up. The mangrove community is represented by four phases dependent on peculiarities of the environment and each characterized by different dominant species.

Phase 1 is found at the heads of creeks where the deposit of mud is very slight and mostly in cracks and depressions. Here *Bruguiera* sp. dominates and with it is associated *Ceriops* sp. The roots of these trees penetrate down into

the fissures of the rock. Aerating branches from the roots of the former rise above the surface as knots and hoops. Phase 2 grows farther down the creeks where the mud deposit is deeper and where the trees are more frequently washed by sea water. This phase is a more or less pure stand of *Rhizophora* sp. Phase 3 of the mangrove formation exists on more open flats where there is a more even but still shallow deposit of mud which is flooded at high tides. This is a pure stand forest of *Avicennia* sp. The trees are rather evenly spaced at 8 m. intervals, and their branches interlace enough to throw a light shade on the ground. The ground is devoid of any other plant growth but is covered with the short perpendicular aerating roots of the *Avicennia*. The last phase of the mangrove formations is not in direct contact with the open lagoon but is found in inland depressions which are scarcely reached by the tide but which become filled with a mixture of brackish water and mud. These hollows may even dry up during the dry season. In the centre of these basins are thickets or clumps of *Lumnitzera racemosa*. Around the edges above the most swampy part grow shrubs of *Hibiscus* sp. above a carpet of *Fimbristylis ferruginea*.

The *Bruguiera* and *Rhizophora* forests are exploited for timber and bark, but regeneration is good and they do not show signs of being destroyed. The mangrove forests eventually die out as a natural result of the weathering away of the atoll rim and the greater exposure of and scouring in the lagoon. The interesting patch of relict mangrove forest which can still be seen in the lagoon of Cosmoledo has already been remarked upon by Fryer (1910).

#### *Psammophilous associations*

The preceding three communities have been correlated with a progressive lowering of the land surface as a result of the wearing down of the limestone rock during the process of weathering. The vegetation now to be considered is, on the other hand, dependent on a piling up of sandy detritus which is derived from the fringing reef. The resulting dune surface which is built up in this way may stand on a base of limestone rock or, as is the case with the sand cay islands, on a base of coarse rubble collected on a submerged bank. The resulting vegetation in each case is the same, and the secondary modifications which will be noticed are dependent on aspect factors. The various communities which belong to this group are often very distinct, and so they are best treated under separate headings as subgroups.

Around the coasts of all the islands, above high-water mark, is a bank of coral sand. Along the more sheltered coasts this bank rises little above sea-level, since the wind has little power to blow it into dunes. On the other hand, the waves during occasional storms may throw up lumps of broken coral. Such beaches are therefore characterized by a slightly raised coastal strip of sand between the shore and the more or less level interior of the island in which will be imbedded large and small fragments of broken coral. Along the exposed coasts, that is, those facing the prevailing south-easterly wind, the

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wave action is more violent, the sand is ground up more finely, and this fine material is piled up by the wind into dunes of considerable height. It is evident that the seaward face of these dunes is exposed to violent and desiccating winds, often to clouds of spray and finally the sand itself is in a constant state of shifting. It is also evident that the landward face of these dunes is sheltered by its own bulk and so here conditions of shelter prevail. These factors all influence the type of vegetation. The south-easterly winds blow with greater force, and during a longer period the nearer one approaches 10° S. Hence the southernmost islands are those with the most marked dune formations.

The bed of coral sand, when covered with vegetation, becomes stained with humus in its upper horizons. If the section of a profile is examined it will be seen that this staining becomes less dark as the depth increases until unstained white sand is reached. When the vegetation is cleared the surface layer becomes leached a pure white colour. On parts of some of the islands there have been large secondary deposits of guano. In the majority of the cases this deposit has been removed, or if not removed the area has been planted up with coconuts, and so in either case the natural vegetation has been removed and consequently these areas need not be considered in the present study.

### *Dune scrub*

The plant community that develops on these areas of sand is a xerophytic scrub of *Scaevola* sp. and *Tournefortia argentea*. The latter plant often dominates, but there is considerable variation in the proportions in which the two species are represented, and it is not very evident what influences the preponderance of one species over the other. The natural shrubs are close set and the plants reach a mean height of about 3 m. The soil is lightly covered with dry leaves and in more open places by clumps of *Fimbristylis obtusifolia*. Scrambling over the shrubs, at times nearly killing them, is the parasitic dodder-like plant *Cassytha* sp. Other plants which are occasional associates are small trees of *Guettarda speciosa* and *Cordia subcordata*.

A very well-marked phase of the above community comes in wherever the area is exposed to excessive wind such as on the windward slopes of the dunes and near the open sea on the windward coasts. This is a thick-set growth of the very xerophytic shrub *Suriana maritima*. *Scaevola* and *Tournefortia* become quite rare or are only represented by dwarfed wind-moulded bushes with extra thickened leaves. The *Fimbristylis* and *Cassytha*, however, persist.

Along the top of the beach of these most wind-swept coastlines in a situation too bleak for any shrubs to survive, there is one more narrow zone of vegetation. This is composed of scattered, half buried, rosette-like plants, namely *Fimbristylis obtusifolia*, *Sida vescoana*, and a *Euphorbia* near to *E. microphylla*.

On banks of recently built-up sand the *Fimbristylis* is again a characteristic plant, and in such places it is associated with the trailing *Ipomea pes-caprae*.

*Spray zone community*

A sharply differentiated and very characteristic variation comes in wherever the coastal edge is bathed in spray. Sand may be thrown up on to the rocks to form a narrow coastal fringe, and where the exposure is considerable and around the mouths of blow-holes there is always a pile of sand and shingle continually moistened with spray. In such places grows a bright green sward of *Sporobolus virginicus*. A few other plants may be present, but these are not confined to the spray zone. In the present site they assume extremely xerophytic characters such as thick fleshy leaves and a dwarfed form. The most constant species in this category is *Ipomea pes-caprae*. In little pockets of soil caught in hollows between the rocks where sea water also collects, which upon evaporation leaves a deposit of salt crystals, only a few extremely halophytic herbs are able to exist.

*Herb mat community*

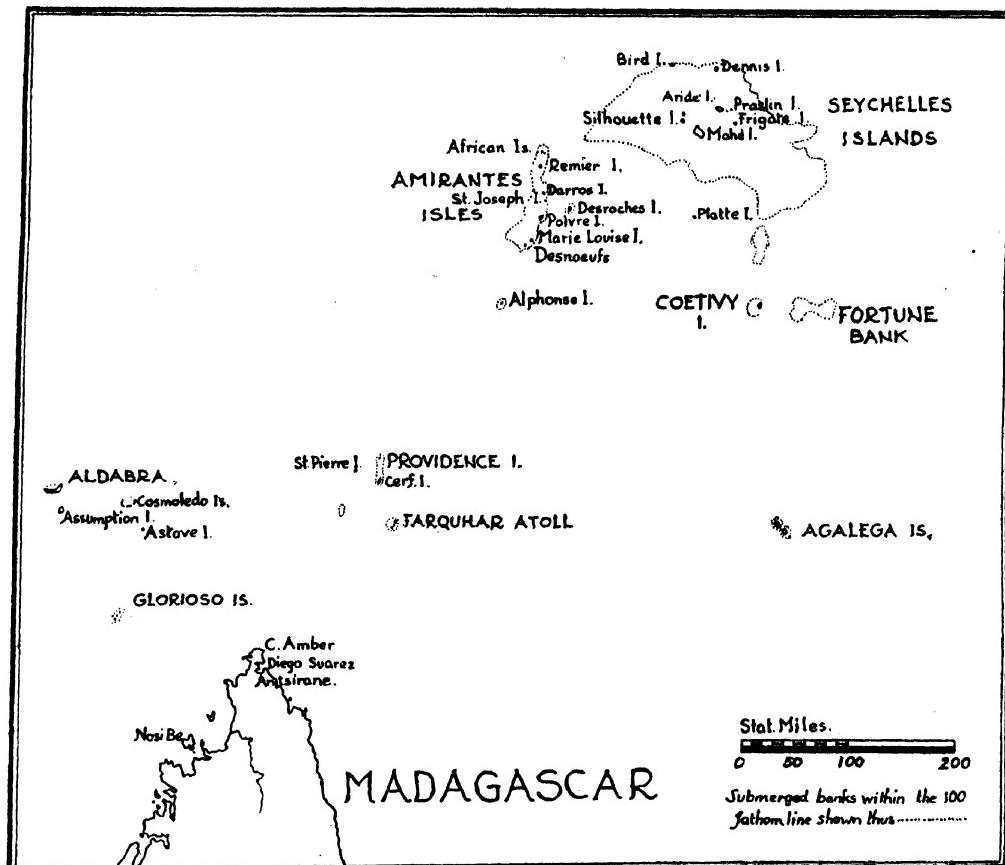
Over areas upon which sea birds nest the above plant-associations, except for the resistant *Sporobolus* sward, are withered up and eventually suppressed. On places where nesting is densest and the trampling most severe the ground is quite bare. At the same time the sand is enriched by the addition of guano, so a luxuriant, seasonal herb mat springs up during the period of the rains which coincides with the period of least activity among the nesting birds. The plants which come up are a mixed assortment of annuals which hardly form a set community but vary in blocks from place to place. The most constant species represented are *Portulaca* sp., *Mariscus rufus*, *Boerhaavia diffusa*, *Achyranthes aspera*, *Stenothaphrum subulatum*, *Dactyloctenium aegyptium*.

## THE ISLANDS

In the foregoing sections the plant communities have been described, and the relations which these bear to modifications in the environment noted. In the present section a brief survey of the peculiarities of the vegetation on certain islands will be undertaken in order to show how these relationships are manifest in the field. It will be evident from the above discussion that these factors which influence the plant associations tend to cause the vegetation to become arranged in definite zones. There are two types of zonation which have to be considered at the same time. The first is dependent on the gradual lowering and changing of the land surface due to the action of weathering agents which brings about a series of concentric zones of vegetation across the atoll rims from the sea to the lagoon coasts. The second is dependent on aspect which causes vegetation of the islands to become arranged in arcs of a circle, namely, a windward arc and a leeward arc. In the case of the atolls further modification is caused by a windward and a leeward lagoon shore having to be brought into account as well.

*Aldabra island*

Aldabra is situated in lat.  $9^{\circ} 22' 35''$  S., and long.  $46^{\circ} 14' 41''$  E. The island is an atoll 25 miles long and from 4 to 10 miles wide, the long axis lying approximately east and west. About 60 sq. miles of island surround a similar area of lagoon. The land is divided into four islands by four passes from lagoon to open sea. Aldabra is the largest land surface considered in the present study, and consequently its vegetation has been least influenced by secondary maritime factors. Hence the mixed scrub is well developed, but the sand dunes



are poorly represented. All the islands are formed of limestone rock, and there is but a scant covering of soil. There are two coastal zones, a narrow strip along the open sea coast and a wider strip round the lagoon coast, of metamorphic rock called locally 'champignon'. On this grows *Pemphis* thicket. These coastal zones surround an area of coralline pavement on which mixed scrub occurs, but as there is here very little soil, the trees are largely confined to the rock crevices and the community is very open.

The most sheltered part of the coast is that to the south-west. The cliffs here are intact, and there is very little sand accumulation. Hence there is no

development of psammophiles, and since the mixed scrub is not restricted by extreme maritime influences it pushes right up to the coast while the *Pemphis* strip is very narrow and indefinite. As the coastline swings round to the south, conditions change very suddenly owing to the increasing exposure. The cliffs are broken down and a strip of barren wave-lashed rock slopes down round the land-level to the sea-level. The pounding of the sea reduces any debris to fine particles and throws these up on to the land where they form a coastal belt. On this a few plants of *Pemphis* exist in a very reduced and wind-swept condition. Likewise a few psammophiles are present, but they are represented by low, thick-leaved plants. The characteristic association of this strip is a sward of spray-drenched *Sporobolus*, and immediately inland of this is a belt of the coarse tufts of *Sclerodactylon macrostachyum*. Inland of this spray zone is rugged pavement, but the land rim is not very wide at this part and so the sea breezes sweep right over the area. As a consequence the mixed scrub which would normally develop on this part is somewhat modified. The species present are limited and the bushes are low and wind moulded, also there is a big incursion of *Scaevola frutescens* and *Guettarda speciosa*. That the aspect and consequent degree of exposure is actually the limiting factor to the vegetation is made evident by following on round the coast. Wherever a small bay is encountered the coast of this which faces the south-west will be marked by a much more luxuriant development of the mixed scrub, and the part facing south-east will be characterized by more extreme xerophytic features.

Continuing along the coast towards the eastern end of the south coast the force of the prevailing wind becomes more pronounced, and more debris is thrown up on the beach and this is blown up into low dunes. There is only a very meagre growth of psammophilous shrubs on these dunes, the dominant plant being *Sclerodactylon macrostachyum*, which forms an open growth of clumps. Behind the coastal strip is again rugged pavement, but so desiccated is the area by sea breezes that the mixed scrub is almost suppressed except in hollows and in its place there is the *Scaevola-Guettarda* association. Inland again behind the rugged pavement is a well-marked zone of 'champignon' with *Pemphis* thicket, and around the lagoon coasts the usual mangrove formations. This part of the lagoon coast is the leeward shore of the lagoon, and it possesses certain features which differentiate it from the windward lagoon coast. The 'champignon' is traversed by numerous creeks, and as the lagoon proper is approached this rock is split off into isolated blocks but not islets. Beyond the fringe of detached rocks are extensive flats of fine white sediment which are left exposed at low tide. No mangroves grow on these tidal flats, but this type of shore is confined to the creeks and open spaces amongst the 'champignon'.

The north coast of Aldabra consists of an almost unbroken line of undercut cliffs which may become penetrated by caves which open inland as blow-holes. Around the mouths of these blow-holes a pile of sand accumulates, and

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the ultimate result of the wearing away of the cave is for the cliff face to collapse and for a sandy beach inside a bay to be formed. The tops of the cliffs are crowned with a fringe of *Pemphis*. Where sand accumulates psammophilous plants gain a footing, one of the first to establish itself being *Cordia subcordata*. Within the *Pemphis* fringe is a luxuriant growth of mixed scrub. With a fall in the level of the land 'champignon' rock with *Pemphis* is encountered, and this forms a zone intersected by mangrove-filled creeks as has been noted in other parts. The lagoon shore which bounds the northern land rim faces south, and so it is the windward lagoon shore. The water along this shore is deeper than along the leeward lagoon shore, and there are no extensive flats of white mud. The lapping of the water is more intense, and this prevents the sediment settling down, and at the same time the 'champignon' is eaten into more rapidly and large blocks become isolated to form offshore 'mushroom-like' islets. From the point of view of their vegetation these islets are miniature replicas of the main land rim. Those that stand up above the level of the lagoon are crowned with a mixed *Sideroxylon-Pemphis* association, and those in a further stage of decay and containing caverns reaching down to sea-level are covered with a growth of *Rhizophora*. In the neighbourhood of the main passes the strength of the tide has scoured out the channels and mangroves are not established; in these circumstances the *Pemphis* reaches to the lagoon edge.

### *Astove island*

Astove is situated in lat.  $10^{\circ} 6'$  S. and long.  $47^{\circ} 45'$  E. The island is an atoll 2 miles long and  $1\frac{1}{2}$  miles wide. Within the land rim is a shallow lagoon with a single pass to the open sea at its south-western end. The land area is said to cover 1604 acres and the lagoon 2974 acres. The island, like Aldabra, is of limestone, but the changes subsequent to its original formation have brought about considerable modifications. The lagoon is extending its area at the expense of the land rim, but at the same time since the single opening to the open sea is not sufficiently large to allow for a free flushing out of the lagoon it is becoming silted up and is consequently becoming shallower. At the same time there has been considerable secondary piling up of coral sand on to the land rim which on the exposed south-east coast rises to form a series of dunes. There was also a considerable deposit of guano on this island and hence a fertile soil. During recent years the exploitation of this guano and at the same time considerable cultivation of maize and coconuts in the more fertile areas have been preceded by the destruction of much of the original vegetation. For this reason the zonation of the flora dependent on the lowering of the level has become somewhat obscured. On the other hand, the zonation of the vegetation depending on the aspect is extremely well marked. The vegetation is arranged into four arcs, namely, a windward sea-coast zone, a windward lagoon-coast zone, a leeward sea-coast zone and a leeward lagoon-coast zone. Traversing the island from the south-east to the north-west all these zones are

crossed. The exposed south-east coastline is marked by a series of dunes reaching a height of some 15 m. The ridge of the dune is not continuous, but it alternates with depressed areas through which the wind sweeps across the land rim. These flatter areas are periodically planted with maize during the rainier and calmer season; the natural vegetation has therefore been replaced by weeds of cultivation. The original plant formations are intact on the dunes proper. The first zone of vegetation, immediately above high-water mark, is composed of scattered, half-buried rosettes of xerophytic herbs. These plants are peculiar to this region of driving sand and they do not represent a true spray-washed formation, since the distance of the reef offshore reduces the amount of spray that reaches this part of the beach. Behind the dunes rise up and they are covered with low wind-moulded shrubs of *Suriana maritima*. Only farther inland or on the lee sides of the dunes is there any considerable incursion of *Scaevola* and *Tournefortia*. The land rim is narrow at this part and the sand has been blown almost right across, but as the lagoon shore is approached there is a strip of 'champignon' rock. Where this rock is sufficiently above the level of the lagoon it is covered with *Pemphis* thicket. The area is, however, very low lying and liable to be flooded at high tide. This area is covered by a deposit of fine mud which is perforated by crab-holes and covered with turret shells. Relict, mushroom-shaped blocks of limestone stand up here and there marking the former level of the land surface. The vegetation of this area is an open *Pemphis* scrub characterized by the very unthrifty condition of the bushes. As the lagoon shore is approached nearer still, and of course this is the leeward coast of the lagoon, the *Pemphis* goes out and is replaced by a bed of halophytic herbs, the latter in its turn going out when the level is so low as to be permanently flooded. There is no mangrove forest on Astove, since these trees do not grow in the white sediment in the open lagoon. There is, however, a rather indefinite ring of scattered trees of *Avicennia marina* just along the edge of high-water mark.

Continuing the traverse across the lagoon, the windward shoreline is reached. The water here is agitated by the wind, and so there is no deposit of fine mud but little wavelets lap up against low undercut limestone cliffs. On windy days this shore is lined with foam. The lagoon sediment is thrown up to form little beaches or low ridges along the tops of the rocks. Small patches of spray-washed *Sporobolus* sward are present along the edge of the shore, and coconuts and *Casuarina* have been planted in places. Along the tops of the rocky edges is a narrow fringe of *Pemphis*, and where sand ridges have been built up a few bushes of *Scaevola* and *Tournefortia*. The north-west end of the land rim is rather narrow, but continuing the traverse across it a zone of coralline limestone is reached which has been cleared of vegetation and supports only scattered bushes and plants of introduced sisal. Beyond this again the leeward coast is reached. All along this coast there is a belt of coral sand which is not piled up by the wind since this area is sheltered from the prevailing

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winds, but it has been thrown up by wave action and therefore large lumps of broken coral are imbedded in the finer sand. This belt has been planted with coconuts, and the original vegetation can only be seen along the sea-shore edge. This is a thicket of *Suriana*, *Scaevola* and *Tournefortia*. Towards the western end the leeward land rim widens out, and here the zone of coralline limestone is much wider than at the point where it was crossed in the foregoing traverse from south-east to north-west. The terrain here is composed of coral rock in which fossil corals in the position of growth can be seen. This area contained rich deposits of guano which formally covered the surface and filled up all the depressions and cavernous pits which occur over the area. The guano has been removed, the exposed rocks are bleached a white colour, and the bottoms of the empty pits contain red mud. The vegetation has been largely cleared during the process of guano extraction. A deciduous scrub covers much of the area, some of the species being characteristic of the mixed scrub formation, but trees of *Pisonia* are also frequent. The rest of the area is covered with a mat of *Plumbago aphylla*.

### *Assumption Island*

Assumption is situated in lat.  $9^{\circ} 46' 20''$  S. and long.  $46^{\circ} 30' 30''$  E. The island is  $3\frac{3}{4}$  miles long and  $\frac{1}{2}$ –1 mile wide. This island has no lagoon. The island is again of limestone, and upon it vast quantities of guano were found and have now been exploited.

A traverse of the island from the windward to the leeward side passes through all the types of vegetation present on the island. The windward coast is lined with a wave-beaten rocky shore, and along the top of these rocks a ridge of sand has been thrown up. This is covered with a sward of *Sporobolus* which is varied in places by clumps of *Sclerodactylon*. Along the most exposed parts of the coast the rocky margin has been beaten down by the waves, and steep sandy beaches cover the rocks. Up these beaches the wind blows and piles the sand into dunes of varying size, the largest reaching a height of 27 m. (90 ft.). The sand of these dunes is in a very mobile state and they are not closely covered with vegetation. The elements of the sand-dune scrub are all present, *Suriana* towards the more windy parts and *Scaevola* and *Tournefortia* where the force of the wind is less strong.

The central area of the island has been largely cleared of vegetation during the exploration for, and exploitation of, the guano. It is now a flattish area of rugged pavement which towards the centre is much broken up into open pits with sea water at the bottom. The whole of this area was more or less covered with guano in the past. A thick secondary mat of *Plumbago* now covers the whole of this country.

The leeward coastal strip along the west coast consists of a belt of coral sand about 100 yd. wide thrown by the waves up against, or on to the top of, the limestone. This strip has been planted with coconuts, and the original

vegetation, namely, psammophilous shrubs, only remains as a fringe along the shore.

*Cosmoledo group*

Cosmoledo is situated in lat.  $9^{\circ} 41' 20''$  S. and long.  $47^{\circ} 32' 12''$  E. The group forms an atoll 9 by 7 miles. The various islands are situated round the rim of the atoll, each one separated from its neighbour by a channel. Originally it must be presumed that the land rim was perfect, and the various islands that exist to-day represent the fragments remaining at an advanced stage in its disintegration. Each island therefore is composed of similar limestone rock but each one presents a different stage of breaking down or building up, and at the same time as one travels round the atoll each island presents different faces to the various aspects. It is evident therefore that a study of these islands is very instructive from the point of view of their vegetation.

The first island that will be studied is Menai Island, which is a crescent-shaped piece of land on the western edge of the atoll rim. The sea coast is convex and the lagoon coast concave. The former, however, having a western aspect is sheltered. Along this coast there is a 100 yd. strip of wave-thrown coral sand and rubble which, except at few places along the shore, overlies and completely conceals the limestone base. This strip has been planted with coconuts and, during the rains, maize is grown. The original vegetation is only seen as a fringe along the coastline. This is of the usual sand-dune scrub type with *Guettardia speciosa* rather frequent. Rounding the extreme south end of the island the shore becomes exposed to the prevailing wind, and the sand is here piled up into small dunes. These dunes are in an active state of development, and the vegetation is a rather open phase of the sand-dune scrub, the bare areas of sand between the plants having a wind-rippled surface. This type of country is that which would be normally expected along an exposed coast, and of course a coast facing such a broad and open lagoon as that of Cosmoledo is nearly as windswept as the open sea coast. Continuing round into the concave face of the east coast, however, there is a change. Sheltering in the bight between the two arms of the crescent is a patch of mangrove forest. This is evidently a relict patch of a fringe of mangrove forest which once must have occurred all round the inside of the lagoon as it does at Aldabra. The part of the east coast of Menai Island still sheltering, and sheltered by, mangrove forest has all the characters of a windward lagoon coast. The 'champignon' rock of the island is intersected with channels, and offshore islets of rock stand out in the lagoon; these channels and rock clusters support a growth of *Rhizophora*. Towards the outside edge of the *Rhizophora* clumps, where the force of the tide is stronger, *Bruguiera* replaces the former. Along the extreme edges of the formation *Avicennia* forms a peripheral fringe.

Continuing up the east coast through the mangroves the face of the extreme northern point of the crescent, which has a south-easterly aspect, is exposed to the prevailing winds blowing across the lagoon. Sand dunes, covered with the

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usual scrub, are therefore again found at this part. As soon as the north point is rounded the characteristics of the west coast, which have already been noticed, are met with again.

Within the coastal zone, forming a narrow central strip, there is 'champignon' rock covered with *Pemphis* thicket, and in the north, some rugged pavement of coralline limestone surrounded by the 'champignon', and bearing mixed scrub.

Leaving Menai Island and continuing northwards round the atoll rim several small islets are passed. These are relict fragments of the former land rim, and the vegetation on them is that noted on similar islets in the lagoon of Aldabra. Those which are raised above the lagoon surface are crowned with a *Pemphis-Sideroxylon* association under which there is a mat of *Plumbago*. Those which are broken down so that pits and caverns reach to sea-level shelter clumps of *Rhizophora*.

At the extreme north point of the atoll rim is West-north Island. This is a narrow strip of land with its axis in north-east to south-west direction. The island is a block of coralline limestone upon which lies a layer of guano which is being exploited, and so the vegetation on this part has been cleared. Along the north-west sea coast, which is sheltered from the prevailing wind, there are low 'champignon' cliffs and small sandy beaches, and on the top of the cliffs is a fringe of *Pemphis*. The opposite coast has a south-easterly aspect, and small dunes have been piled up over the rock; on these grows the usual scrub of *Tournefortia* and *Scaevola*. Immediately above high-water mark on this shore are patches of *Sporobolus* sward.

Continuing round the atoll rim the next island of importance is Polyte. This island is slightly crescent-shaped, with its concave face towards the lagoon and its long axis in a north-south direction. At the extreme south point the 'champignon' rock is being eaten away, and so while the tops of the blocks are crowned with windswept shrubs of *Pemphis* the caverns reaching down to sea-level are filled with *Avicennia*. Behind this rocky point the sand has been piled up into small dunes which, being exposed to the full force of the wind, are covered with *Suriana* shrubs. Continuing up the west side of the island the coast gradually bears round towards the north-east, and in so doing becomes more sheltered. The dunes do not therefore continue all the way up along this coast but become smaller until only a coastal ridge of wave-thrown sand crowns the rock and eventually uncovered cliffs of 'champignon' occur along the shoreline. The sand ridge is covered with a sward of *Sporobolus* and the uncovered rock with *Pemphis*. The lagoon coast of this island is sheltered and is formed of undercut 'champignon' cliffs, and along the whole of this there is *Pemphis*.

South of Polyte Island is Wizard Island, which is a large slightly crescent-shaped strip of land with its long axis in a north-north-east to south-south-west direction. The seaward coast is exposed to the full force of the prevailing

wind. The shoreline is of much broken-up rock, and immediately behind rises a series of dunes. Just above the shoreline the foot of the dunes is bathed in spray, and this zone is covered with a sward of *Sporobolus*. The face of the dunes exposed to the sea is covered with pure *Suriana* shrubbery. On the leeward face of the dune *Tournefortia* becomes mixed with the former. At the extreme south end of the island there is uncovered 'champignon' rock on which grows a very wind-swept *Pemphis* thicket. Under the lee of the dunes is a belt of coralline limestone with guano deposit. This is the site of a large ternery, and also there has been maize cultivation here, so the original vegetation has been modified. The lagoon coast is sheltered, and this area is covered with seasonal herb mat which comes up after the birds have left. The actual shoreline is composed of 'champignon' cliffs with *Pemphis* bushes.

Continuing round the atoll rim the next land is South Island. This is a narrow strip of land with its long axis lying in an east-west direction. Only the extreme eastern point is exposed to the prevailing wind, so it is only here that a small dune has been piled up. At the extreme western end the curve of the land causes the lagoon shore to face the east, and the wind sweeping along the lagoon flats has built up a little dune of lagoon sediment at this point. Both these little dunes support psammophilous shrubs. All along the south coast which faces the open sea there is a fringing ridge of detritus thrown up by the waves, and on this grow shrubs of *Suriana* and small trees of *Pisonia*. The northern lagoon shore is formed by undercut limestone cliffs and offshore stand mushroom islets. Inland extend creeks which in places nearly cut the island across. Inside these creeks are trees of *Avicennia* and a few *Rhizophora*. The centre of the island is rugged limestone rock upon which many sea birds nest. As a consequence the rock lies exposed over much of the island, but in more sheltered hollows and elsewhere there are small bushes of *Pemphis*, *Sideroxylon* and *Euphorbia* sp.

#### *St Pierre Island*

St Pierre is a round island of limestone rising some 15 ft. above sea-level and covering an area of 410 acres, situated about 270 miles east by Aldabra. The island was covered with a rich deposit of guano which is now being exploited, and so the original vegetation has now been all cleared away. Relict trees of *Pisonia grandis* and *Euphorbia abbottii* probably represent the last of the original vegetation. Now the surface of the island is covered with a mixed herb mat. The coasts of the island have been little broken down, and so there has been very little secondary piling up of coral sand. The cliffs of the windward coast are deeply undercut and in places penetrated by blow-holes. Around the mouths of these, piles of sand collect, and on these grow *Sporobolus* sward. Round the leeward coast there is a small irregular ridge of wave-piled sand, and a thin much-interrupted fringe of *Suriana-Tournefortia* or *Pemphis*.

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### SUMMARY

The vegetation of characteristic islands in the Indian Ocean is described and related to the stages of denudation of the original limestone rock and to the degree of exposure to prevalent winds and wave action.

On the least denuded areas of rocky 'pavement', a mixed scrub dominated by *Sideroxylon inerme* is found, changing to a thicket of *Pemphis acidula* where the rock has been eroded into 'champignon' forms. Mangroves occur in sheltered lagoons on muddy detritus from this erosion.

The more exposed shores may develop calcareous sand dunes with dune scrub (mainly *Scaevola* sp. and *Tournefortia argentea*) if sufficiently stable. Where spray-moistened sand or shingle occurs, a sward of *Sporobolus virginicus* is found, and a mat of mixed herbs characterizes areas occupied by guano-forming birds. The guano deposits, now mostly removed, also affect existing vegetation.

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# ECOLOGICAL ASPECTS OF PEAT ACCUMULATION

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(*With eighteen Figures in the Text*)

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### I. INTRODUCTION

BOTH in this country and on the continent the study of peat deposits has provided valuable evidence concerning the changes in climate and vegetation which have occurred during post-glacial times. It has become clear that a more certain interpretation of many of the features of the general structure of peat mires and their stratigraphy depends essentially on critical ecological studies of the plant communities developed on these sites. Such studies are seriously hampered in this country by the manner in which many of the peat deposits have been modified by artificial drainage and peat cutting, so that their vegetation retains little of its natural character. The interest of two small peat mires in the north central Pennines, Thornton Mire and Hukermire Moss, was therefore enhanced by the fact that their isolated position had protected them from the cruder forms of human interference. Each of these mires contains a complex assembly of plant communities which appear to be closely

integrated by the conditions under which they are developed. It has seemed valuable therefore to attempt an elucidation of the more important factors which have combined to produce this mosaic of communities.

The present account is confined to a description of the vegetation and the ecological conditions at present prevailing in Thornton Mire: a short account is given of the structure and distribution of the peat deposits in so far as this is relevant to a discussion of the main conditions which have influenced the accumulation of peat in this Mire.

## II. TOPOGRAPHY AND CLIMATE

The position of Thornton Mire is shown in Fig. 1. It lies upon a narrow neck of high ground at about 385 m. (1260–1270 ft. o.d.), connecting the main watershed of Stake Fell (487 m.) with Addleborough (357 m.), which is a spur jutting northwards into Wensleydale. Another small mire, Hukermire Moss, lies on a shelf of the north-facing slope of Addleborough, parallel to Thornton Mire.

The two mires, Thornton Mire especially, lie in troughs which bear no direct relation to the present drainage of these hills. Sections 1 and 2, drawn from the Ordnance Survey contours along the lines marked 1 and 2 in Fig. 1, show that Thornton Mire, far from receiving drainage of any magnitude in the direction of its slope, which might account for the excavation of the channel with steep north- and south-facing sides, receives only surface drainage from the slopes of Addleborough and Stake Fell.

An interpretation of this topography is due to Kendall & Wroot (1924), and later to Raistrick (1926), who have demonstrated that during the late phases of the last glaciation, the Wensleydale glacier blocked the exits of the tributary valleys of the main dale. These valleys contained deep lakes, the water of which was derived from the melting ice and snow on the watersheds. The escape of the summer flood took place in a direction parallel with the glacier either by way of channels between the sides of the glacier and the watershed, or across weak points between spurs and the main watershed. Hukermire Moss is a channel of the first, and Thornton Mire a channel of the second type: by means of them, flood water from Lake Semerdale escaped eastwards into Lake Bishopdale, which was maintained at a slightly lower level.

The valley floor of Thornton Mire is not simple, owing to complications arising out of temporary advances of ice during the main phase of retreat. The result of one of these advances seems to have been the formation of a small lateral moraine across the mouth of the channel where it emerged into Bishopdale. Later the channel again became functional, and the moraine was partly removed by flowing water, but drainage, both of lake flood water, and later of water from the hillsides, was impeded to some extent.

The floors of Thornton Mire and Hukermire Moss are now occupied by deposits of peat, in places reaching a depth of about 3 m. This is common in

such drainage channels in the north of England, as has been indicated by Kendal & Wroot, and Elgee (1912), and it is these peat deposits which form the subject of the present study, which deals with the history and floristic composition of the vegetation of Thornton Mire.

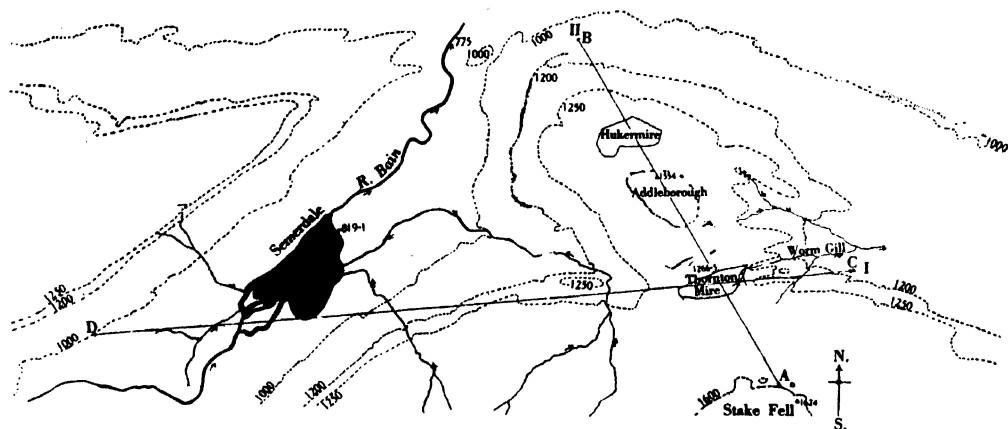


Fig. 1. Map drawn from the 6 in. Ordnance Survey to show the position of Thornton Mire (T.M.), and Hukermire Moss (H.M.). The contours (dotted lines) of 1150, 1200, and 1250 ft. only are shown.

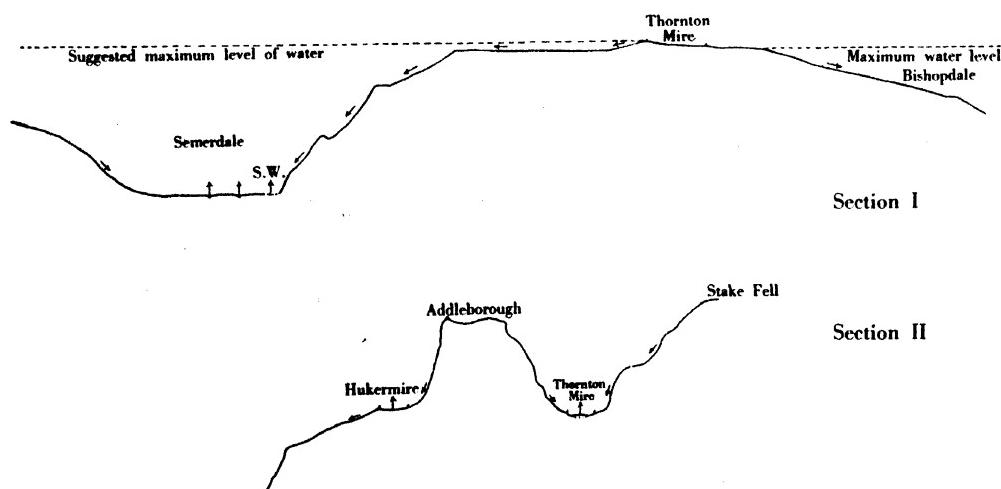


Fig. 2. Two sections constructed from the Ordnance Survey map to show the position of Thornton Mire in relation to the present drainage system of Wensleydale. The position of the sections 1 and 2 is shown in the map Fig. 1.

The mire occupies the base of a steep-sided valley, with a narrow entrance at the west end. The maximum height of the floor here is 387 m., and the valley has a gradual slope from west to east. The east end is not simple, but complicated, as has been pointed out, by the secondary moraine, in the form of a raised band of morainic material running east and west. The exit is thus

broken into two parts. The southern part is a wide valley, the head of which lies at 381 m. o.d., and probably was functional as an escape of water, during the later phase of Thornton Mire, as an overflow. The northern outlet is narrow, and has very steep sides somewhat eroded by water: it seems likely that it was deepened, in part at any rate, by later water flow, derived from the hillside after the channel fell into disuse as an overflow from Semerlake.

This latter view is strengthened by a consideration of the structure of the valley sides, where there are at least four disused watercourses, which must have been in the nature of waterfalls. Three flowed down from Stake Fell, and one from Addleborough. The existence of these demonstrates that at some phase the valley must have received a considerable volume of rapidly flowing water, which would greatly affect the configuration of the valley floor, especially at the east end, and may have resulted in a considerable change in the course of the contours, and the depth of the northern outlet.

The climate of the district at the head of Wensleydale, where the mire lies, has not been studied in detail. The main features of the annual rainfall and temperature are to be found in *British Rainfall* and elsewhere. According to Bilham (1938), the district in general has a rainfall of between 127 and 203 cm. (50–80 in.) a year, but this may well be exceeded on high ground. Rain falls on about 200 days a year. The nearest stations to Thornton Mire at which observations on the rainfall have been taken are at Askriigg, about 5 miles (8 km.) from Thornton Mire, at 204 m. (670 ft.) above sea-level in the bottom of Wensleydale, and at Hawes Junction 343 m. (1125 ft.) above sea-level, about 10 miles (16 km.) westward. The records have not been consistently kept, but agree fairly well with Bilham's data.

		In. per annum	Days rain 0·01 in.	Days rain 0·04 in.
1932	Askriigg	47·98	174	146
	Hawes Junction	72·47	191	150
1935	Askriigg	49·76	209	168
	Hawes Junction	—	—	—
1936	Askriigg	43·0	192	168
	Hawes Junction	70·88	—	—
1937	Askriigg	33·96	198	168
	Hawes Junction	52·17	—	—
1938	Askriigg	48·52	223	179
	Hawes Junction	104·92	—	—

The Mire lies at about 385 m., so that the Hawes Junction readings probably approach more nearly to its conditions, indicating an average of about 180–190 cm.

The rainfall is generally distributed throughout the year, but there is a marked summer maximum in August as well as a winter maximum.

The detailed studies of the 'Alton Block' in the North Pennines made by Manley (1936) and Glasspole add further to the knowledge of the district, although they deal strictly with Teesdale where the fell area, em-

bracing Dutton Fell, Mickle Fell and Cross Fell, forms a great plateau which may greatly affect the climatic features. The rainfall, however, is somewhat similar to that of the head of Wensleydale, so that there may be a resemblance in other respects. An interesting feature is that the Cross Fell area has the coldest climate in England, and approaches in temperature the coastal districts of Iceland. Manley suggests on the basis of his monthly readings that abnormally dry months show increases in temperature far outside expectations. And so it follows that a small swing of general climate to drier conditions may well result in a fundamental amelioration of temperature conditions.

These data clearly indicate that the Wensleydale area is one in which the active accumulation of peat would be expected, provided temperature conditions are satisfactory, and one in which small climatic change may have a great effect on the rate of growth of bog plants.

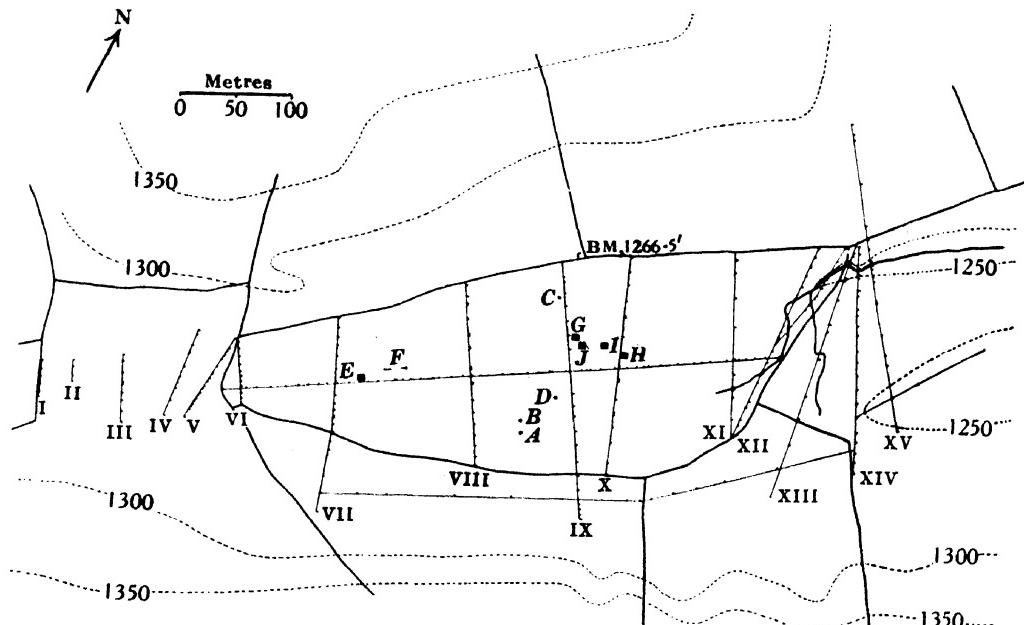


Fig. 3. Map of points determined instrumentally and used in surveying surface level and peat distribution in the channel. The walls are shown by continuous black lines, and the transects with determined points are indicated thus: [ ]. Transects running across the Mire are numbered from west to east, I–XV. The longitudinal transect running within the walls is that mentioned in the text, and the position of plotted quadrats and levelled sections is indicated by letters A–J. Contours dotted from the Ordnance Survey.

### III. METHODS

The investigations were carried out by several parties of observers in the years 1935–9. Thornton Mire valley was carefully surveyed, first by triangulation and later by level and tacheometer. At the survey points borings were made, either with a simple auger or with a Hellier sampling auger. By this means contour maps both of surface and floor levels were constructed.

The vegetation was mapped along the transects of surveyed points, and the main communities represented with a fair degree of accuracy upon a large-scale map. Detailed study of typical parts of each community was made by means of quadrats from 1 to 25 sq. m. in size according to the site. Bisects across the large quadrats were usually levelled instrumentally using water level as arbitrary zero.

The map (Fig. 3) indicates the positions determined instrumentally, at which detailed observations of level, vegetation, peat depth and water table were made. It will be noted that the majority of these points lie within the walls surrounding the main peat deposit, so that here the maps are most accurate. Triangulated points are not shown, since they were used, in the main, for the fixing of salient points in the transition from one community to the next in the mapping of the vegetation. The positions of the plotted quadrats are indicated as squares with the appropriate letter beside each.

Information concerning the stratigraphy of the peat was obtained mainly by digging large pits to 2·8 m. in depth, down to the floor level. In positions of high-water table where digging was impracticable, it was necessary to rely upon borings made with the sampling augur.

Estimations of the pH of samples of water and peat were made by means of a B.D.H. Capillator, both in the field and under laboratory conditions. Some estimates of calcium content of the water were made upon samples brought back to the laboratory, by Mr A. H. Cripps.

#### IV. VEGETATION

The vegetation at present covering the surface of the channel may be conveniently classified as follows:

- I. The communities of the marginal slopes.
  - (a) Grassland.
  - (b) Callunetum.
  - (c) Juncetum communis (agg.).
- II. The communities of the Mire surface.
  - (a) Juncetum acutiflori.
  - (b) Sphagnetum.
    - (i) With *Juncus acutiflorus*.
    - (ii) With *Carices*.
    - (iii) With *Eriophorum angustifolium* and *E. vaginatum*.
  - (c) Callunetum.
  - (d) Communities associated with peat cuttings.

Most attention has been devoted to a study of the vegetation of the Mire itself, but some information, which has been collected concerning the communities of the surrounding slopes, will be briefly set out.

### A. Spatial distribution of the chief plant communities

A map showing the distribution of the main communities of the Mire and the adjoining slopes is reproduced in Fig. 4. The accuracy with which the map could be constructed, varies in different parts; as already stated, the vegetation of the higher slopes was not investigated as fully as that of the Mire, and in these regions the map is derived mainly from field notes, sketches and photographs. On the lower slopes, and on the Mire itself, a large number of points determined instrumentally were available for mapping. No attempt is made to show in detail the different communities into which the Sphagnetum of the mire has been subdivided. While these communities can be recognized as

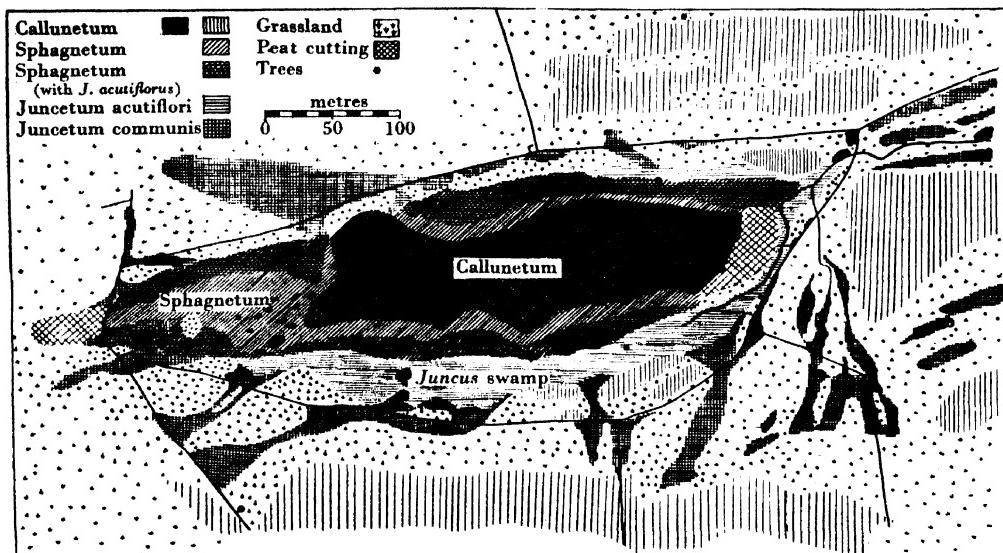


Fig. 4. Map to show the distribution of the chief plant communities of the Mire.

zones bearing a constant relationship one with another, in certain parts they often form a complex intermixture which cannot be represented adequately on the map.

The Callunetum of the Mire occupies a fairly well-defined central area. For a short distance on the north side, close to T. VIII, the *Calluna* extends almost to the grassy slopes of Addleborough, the transition being marked by smaller tussocks of *Eriophorum vaginatum*, less extensively overgrown by *Calluna*. Elsewhere, the Callunetum is surrounded by a region characterized by abundance of growing Sphagna which commonly form an almost continuous ground layer. The extent of this Sphagnetum varies in different parts: at the western end it occupies a broad central band extending up the channel, while along the sides of the Callunetum and at the eastern end it forms a much narrower zone.

Over small areas at the extreme eastern and western ends of the Mire there is evidence that the vegetation has been modified by peat cutting. From local information it is probable that the cuttings at the eastern end have been abandoned for the past 15–20 years, and it seems certain that *Sphagnum* beds, often regular in shape, have developed in pools so formed. Associated with the excavated hollows are drier peat banks supporting vegetation of a distinctive nature. The more recent peat cuttings of the western end have many similar features, although here the hollows are only partially overgrown with *Sphagnum*, and still contain open water.

The marginal communities of the Mire are usually dominated by *Juncus acutiflorus*, often merging gradually into the *Juncetum communis* on the lower slopes. The development and character of the *Juncetum acutiflori* is closely correlated with local conditions of drainage. In positions where little direct surface drainage enters the Mire, the marginal *Juncus* communities may be little developed or absent, such as at the west end, or on the northern margin close to T. VIII. Where there is more active drainage the vegetation takes the form of a *Juncus* swamp, while under intermediate conditions *Sphagnum* may dominate the ground layers. *Juncus* swamp occurs most widely down the southern side of the Mire, under the influence of drainage from Stake Fell. On the northern side a much narrower belt of similar vegetation is usually present, but here *Sphagnum* plays a much more important part in the ground layers of the zone dominated by *Juncus acutiflorus*.

It is clear that in distribution the *Sphagnetum* generally occupies a position between the swamp vegetation of the margin and the central *Callunetum*. The varied aspect of the vegetation in this intermediate zone arises from the variety of other plants with which the *Sphagna* are associated. In many places the following transitional changes may be observed in passing from the margin of the Mire to the centre:

- (a) *Juncetum communis* of the marginal slope.
- (b) Swamp vegetation dominated by *Juncus acutiflorus*.
- (c) *Sphagnetum* with *Juncus acutiflorus* and abundant *Carex inflata*.
- (d) *Sphagnetum* with *Carex inflata*.
- (e) *Sphagnetum* with small tussocks of *Eriophorum vaginatum*, and intervening hollows with *E. angustifolium*.
- (f) *Callunetum*.

The frequencies of the dominant species along a levelled transect, passing from the south margin across the Mire close to T. X, are summarized in Fig. 5 to show the zonation of the above communities at this point.

Owing to the frequency with which it is overgrown by *Calluna* there is a tendency to underestimate the importance of *Eriophorum vaginatum* in the structure of the vegetation of the Mire. Tussocks of this plant are widely distributed throughout the central area, especially in the *Sphagnetum* at the western end, and in the marginal parts of the *Callunetum*.

There are at present five small willow trees, *Salix cinerea*, growing on the Mire: the older ones are stunted (3–4 m. high) and have wind-cut crowns, no doubt associated with the altitude and exposure to westerly gales. The position of the larger trees is near the edge of the Callunetum, while the two younger ones (1–2 m. high) are established in the *Juncus* swamp.

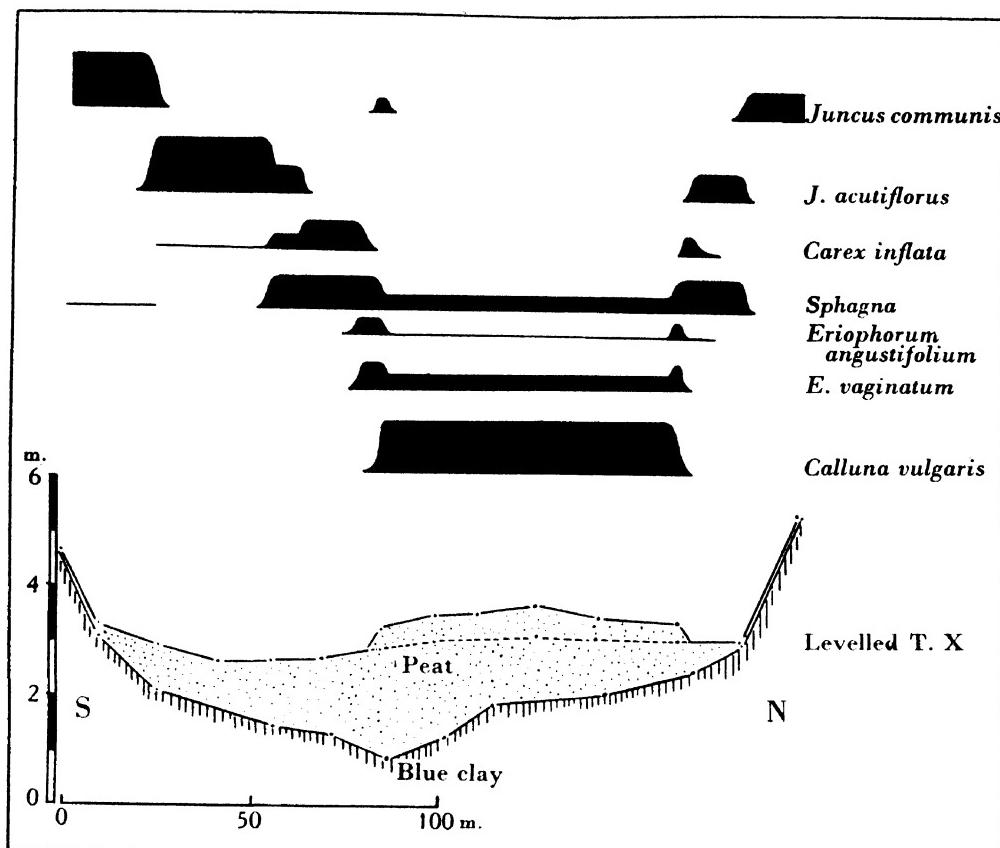


Fig. 5. The zonation of the vegetation along a levelled transect across the Mire. In the upper part of the figure the relative frequencies of different dominant and co-dominant species are shown, and below is the peat profile and levels along the transect.

On the neighbouring sides of the channel, grassland occurs chiefly on the gentler slopes. The soil, especially adjacent to the Mire, is developed on blue-brown clay, and there is relatively little accumulation of humus, the *pH* of the surface layers being 5.8–6.0. The steeper slopes, often of a loose rocky character, are usually dominated by *Calluna* with an abundance of *Empetrum nigrum*, especially in the rough morainic deposits at the eastern end; here there is an accumulation of 1–2 dm. of black amorphous peat having an acid reaction close to *pH* 4.5. Soil conditions and effects of leaching seem to have an important influence in controlling the distribution of *Calluna* and grassy slopes surrounding the Mire. Where more active surface drainage occurs, the

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vegetation is dominated by tussocks of *Juncus communis* (agg.), which may extend some distance up the slopes, although they occur more extensively in the lower regions, and often merge gradually into the *Juncetum acutiflori* of the Mire. At the south-east end of the channel there is an extensive area of very gradual slope, covered with tussocks of *Juncus communis* with intervening patches of grassland. Only a thin layer of peat overlies the blue clay over most of this part, and some artificial drainage is maintained both in the direction of the stream leaving the Mire and down the southern branch of the main channel.

Full lists were not obtained in the Callunetum of the slopes, but in the grassland and *Juncetum communis* the following species were recorded at various points surrounding the Mire:

(1) *Grassland.*

<i>Nardus stricta</i>	l.d.	<i>Festuca ovina</i>	l.a.
<i>Holeus lanatus</i>	l.co-d.	<i>Hieracium sp.</i>	r.
<i>Carex leporina</i>	l.co-d.	<i>Molinia caerulea</i>	l.
<i>Juncus communis</i> (agg.)	l.co-d.	<i>Polygala vulgaris</i>	r.
<i>Galium saxatile</i>	a.	<i>Potentilla erecta</i>	f.
<i>Anthoxanthum odoratum</i>	l.f.	<i>Ranunculus Flammula</i>	o.l.
<i>Cerastium vulgatum</i>	l.f.	<i>R. repens</i>	r.
<i>Rumex Acetosa</i>	o.-l.a.	<i>Sagina sp.</i>	r.
<i>Erica cinerea</i>	o.	<i>Trifolium repens</i>	a.
<i>Eriophorum vaginatum</i>	r.	<i>Valeriana dioica</i>	r.

*Bryophyta*

<i>Brachythecium purum</i>	o.	<i>Mnium sp.</i>	o.
<i>Hylocomium squarrosum</i>	o.	<i>Polytrichum commune</i>	l.
<i>Hypnum cypresiforme</i>	o.	<i>P. formosum</i>	l.
<i>Mnium undulatum</i>	o.	<i>Sphagnum sp.</i>	r.

(2) *Juncetum communis.*

<i>Juncus communis</i> (agg.)	d.	<i>Potamogeton natans</i>	l.a.
<i>Galium saxatile</i>	a.	<i>Cnicus palustris</i>	r.
<i>Anthoxanthum odoratum</i>	o.	<i>Ranunculus acris</i>	o.-r.
<i>Comarum palustre</i>	r.	<i>R. Flammula</i>	l.
<i>Deschampsia flexuosa</i>	o.	<i>Rumex Acetosa</i>	l.a.
<i>Epilobium palustre</i>	r.	<i>Stellaria sp.</i>	r.
<i>Eriophorum vaginatum</i>	r.	<i>Taraxacum officinale</i>	r.
<i>Galium uliginosum</i>	o.	<i>Valeriana sp.</i>	o.
<i>Juncus acutiflorus</i>	l.a.	<i>Viola palustris</i>	o.
<i>Potentilla erecta</i>	f.		

*Bryophyta*

<i>Hypnum cuspidatum</i>	l.a.	<i>Polytrichum formosum</i>	l.a.
<i>Polytrichum commune</i>	l.a.	<i>Sphagnum sp.</i>	l.a.

*B. Juncetum acutiflori*

Under normal spring and summer conditions the water level in this community is maintained above the surface, the flow being slow, and almost imperceptible in drier seasons. According to information from Mr Balmer, the water table is also above the surface in winter. The dominant plant forms a dense

growth, often over 200 flowering shoots per sq. m., and 0·5–1·0 m. tall, while the strong branched rhizome system constitutes an unstable floating mat which undulates markedly under foot. The associated species usually form a lower layer closer to the water surface, and some of them may be floating or submerged. A list of the species recorded in this *Juncus* swamp is given below,

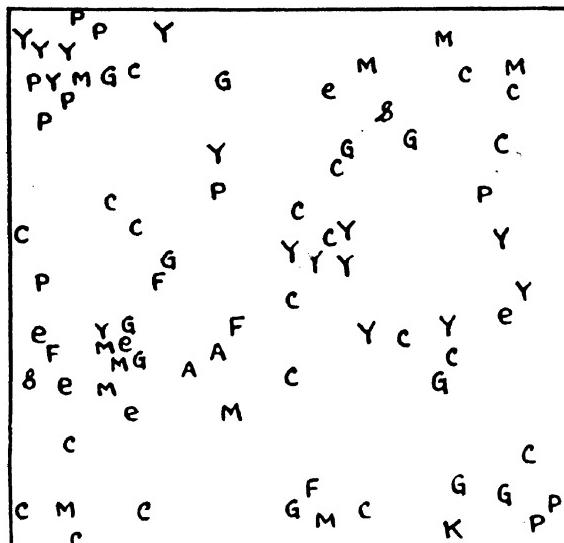


Fig. 6. A 1 m. quadrat in the *Juncetum acutiflori* on the south side of the Mire, position A on map, p. 21. *Juncus acutiflorus* was distributed throughout the quadrat and is omitted from the figure; 215 flowering shoots were recorded. Key to symbols on p. 56.

the estimates of frequency (as with other communities on the Mire itself) being derived from several lists taken at different parts.

<i>Juncus acutiflorus</i>	d.	<i>Juncus squarrosum</i>	r.
<i>Menyanthes trifoliata</i>	f.-l.co-d.	<i>Luzula campestris</i>	o.
<i>Achillea Ptarmica</i>	o.-f.	<i>Lychnis Flos-cuculi</i>	r.-o.l.
<i>Agrostis</i> sp.	r.	<i>Mentha aquatica</i>	f.
<i>Anagallis tenella</i>	l.a.	<i>Mnium affine</i>	l.
<i>Caltha palustris</i>	f.	<i>Mnium</i> sp.	r.
<i>Cardamine pratense</i>	o.-l.	<i>Myosotis palustris</i>	o.
<i>Carex echinata</i>	o.	<i>Pedicularis palustris</i>	r.
<i>C. inflata</i>	r.	<i>Potentilla erecta</i>	o.-l.a.
<i>Cerastium vulgatum</i>	o.	<i>Potamogeton natans</i>	l.a.
<i>Cnicus palustris</i>	r.	<i>Prunella vulgaris</i>	r.-o.
<i>Comarum palustre</i>	f.	<i>Ranunculus acris</i>	o.-f.
<i>Crepis paludosa</i>	r.	<i>R. Flammula</i>	o.-f.
<i>Cynosurus cristatus</i>	l.a.	<i>Rumex Acetosa</i>	o.-l.a.
<i>Epilobium palustre</i>	f.	<i>Stellaria</i> sp.	o.
<i>E. montanum</i>	o.	<i>Scabiosa succisa</i>	r.
<i>Equisetum</i> sp.	f.-l.a.	<i>Sphagnum</i> spp.	r.
<i>Eriophorum angustifolium</i>	r.	<i>Trifolium repens</i>	o.-f.
<i>E. vaginatum</i>	r.	<i>Valeriana dioica</i>	f.
<i>Fontinalis antipyretica</i>	l.a.	<i>Veronica scutellata</i>	r.-l.f.
<i>Holcus lanatus</i>	o.	<i>Viola palustris</i>	f.
<i>Juncus communis</i>	l.a.		

From these lists it is clear that many of the plants of this community are eutrophic species commonly found under 'fen' conditions.

On the southern side of the Mire the swamp is usually 10–20 m. wide, but on the northern side, although a zone of *Juncus acutiflorus* occurs, Sphagna play a much more important part in the ground layer, and the eutrophic species are much less abundant. However, a narrow channel can usually be distinguished 1–2 m. wide, and supporting a vegetation very similar to that of the southern side. A 1 m. quadrat plotted in a typical part of the *Juncetum acutiflori* along the south margin is shown in Fig. 6.

Towards the eastern end where the flow of the water becomes more rapid and confined between peat banks, *J. acutiflorus* is limited to the banks of the stream. On the inner bank, adjacent to the Callunetum, the ground layer is dominated by Sphagna, while the vegetation of the outer one resembles that of the *Juncus* swamp in many respects, although the water table is not maintained at the surface under normal spring and summer conditions. In the stream itself, *Potamogeton natans*, *Fontinalis antipyretica*, and *Mentha aquatica* are locally abundant.

### C. *Sphagnetum*

In nearly all parts of the Sphagnetum the most widely distributed of the Sphagna is *Sphagnum recurvum*. Typically, this species forms a soft and unstable moss carpet, with the even surface of growing shoots raised 5–10 cm. above water level. *S. cuspidatum* is plentiful, growing partly or entirely submerged in pools and hollows protected from the direct influence of drainage. A few scattered tussocks of *S. papillosum* occur locally along the northern margin of the Callunetum, but, although Sphagna of the Cymbifolium group are frequently present in other parts of the Sphagnetum, there is little evidence of active building of raised moss tussocks elsewhere.

In the marginal zone of the Sphagnetum, where it is associated with *Juncus acutiflorus*, *Sphagnum recurvum* commonly forms an almost continuous and partially floating ground layer. The growth of the *Juncus acutiflorus* is here much less vigorous as compared with that of the swamps; there are usually less than 100 flowering shoots per 1 sq. m., and the height of the shoots rarely exceeds 0·5 m. The transitional nature of the vegetation of this part of the Sphagnetum is everywhere apparent: where the *Sphagnum* forms a less continuous ground layer, many of the eutrophic species characteristic of the swamp occur, while Carices typically associated with more central regions are often abundant. Two 1 m. quadrats plotted in this part of the Sphagnetum are shown in Figs. 7 and 8. The first was taken at the south side of the Callunetum, and the second at the north margin as shown in Fig. 3. A list of the species recorded from this community is given below.

#### (i) *Sphagnetum with Juncus acutiflorus.*

*Sphagnum recurvum*  
*Juncus acutiflorus*

co-d.  
co-d.

*Achillea Ptarmica*  
*Agrostis sp.*

r.  
l.

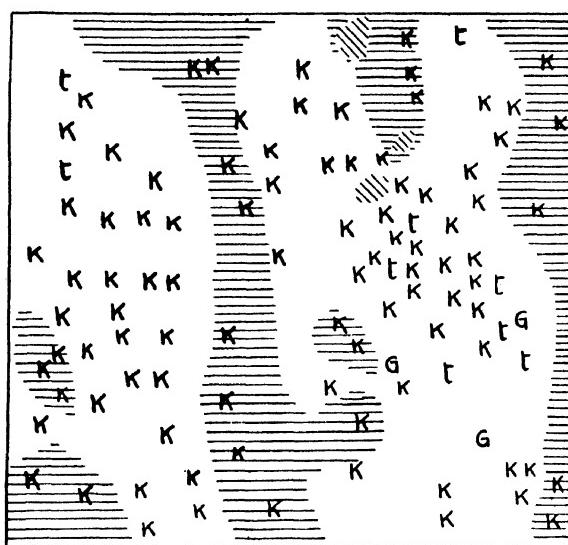


Fig. 7. A 1 m. quadrat in the Sphagnetum with *Juncus acutiflorus* (position B on map, p. 21): *Sphagnum recurvum* and *Juncus acutiflorus* are distributed throughout the quadrat and are omitted from the figure (112 flowering shoots of *J. acutiflorus* were recorded). Where the moss forms a continuous ground layer raised slightly above water level it is indicated by shading. Key to symbols on p. 56.

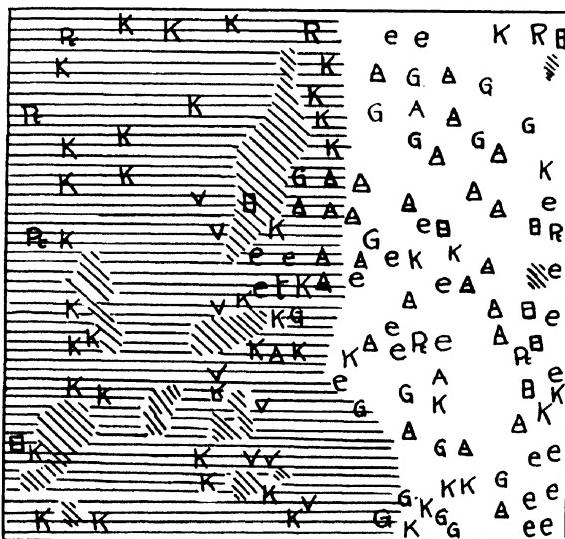


Fig. 8. A 1 m. quadrat to show the transition from the narrow swamp at the north margin to the Sphagnetum with *Juncus acutiflorus* (position C on map, p. 21). The distribution of *Sphagnum recurvum* is shown by shading and *Juncus acutiflorus* is omitted. Key to symbols on p. 56.

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<i>Anagallis tenella</i>	l.	<i>Menyanthes trifoliata</i>	r.
<i>Caltha palustris</i>	o.	<i>Mnium undulatum</i>	l.a.
<i>Carex inflata</i>	l.a.	<i>Potentilla erecta</i>	o.
<i>C. Goodenowii</i>	r.	<i>Polytrichum sp.</i>	o.-l.a.
<i>C. echinata</i>	o.-r.	<i>Potamogeton natans</i>	l.
<i>Comarum palustre</i>	f.	<i>Ranunculus acris</i>	r.-o.l.
<i>Epilobium palustre</i>	o.-r.	<i>R. Flammula</i>	o.
<i>Equisetum limosum</i>	f.-l.a.	<i>Rumex Acetosa</i>	r.
<i>Eriophorum angustifolium</i>	r.	<i>Scabiosa succisa</i>	r.
<i>E. vaginatum</i>	r.	<i>Sphagnum cuspidatum</i>	l.a.
<i>Galium uliginosum</i>	f.-l.a.	<i>S. cymbifolium</i> (agg.)	l.co-d.
<i>Holcus lanatus</i>	r.	<i>Trifolium repens</i>	r.
<i>Hypnum cuspidatum</i>	r.	<i>Valeriana dioica</i>	r.-o.-l.f.
<i>H. dendroides</i>	r.	<i>Veronica scutellata</i>	o.
<i>Juncus communis</i> (agg.)	o.	<i>Viola palustris</i>	f.
<i>Luzula campestris</i>	o.	<i>Juncus squarrosum</i>	r.
<i>Lychnis Flos-cueuli</i>	r.		

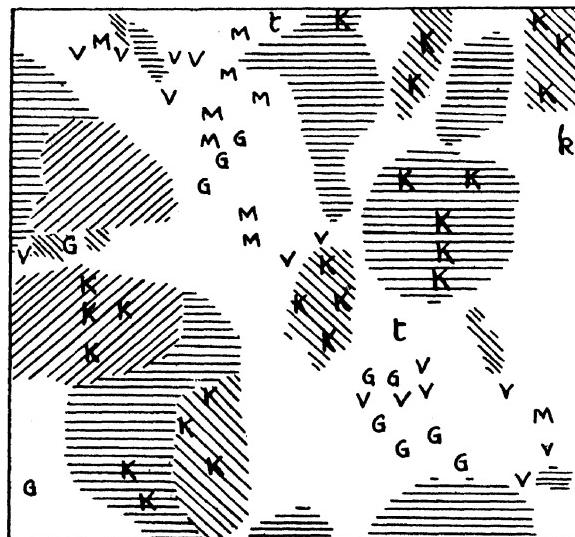


Fig. 9. A 1 m. quadrat in the Sphagnetum with *Carex inflata* (position B on map, p. 21). *Sphagnum recurvum* and *Carex inflata* are distributed throughout the quadrat; a continuous mosslayer raised above water level is shown by appropriate shading and *C. inflata* is omitted from the figure except in shaded areas. Key to symbols on p. 56.

The more central regions of the Sphagnetum are characterized by the abundance of Carices. *Carex inflata* and *C. Goodenowii* are the most conspicuous species, but in some parts, and especially where the Sphagna form a dense and continuous ground layer, the Carices do not flower and fruit freely, so that their identification is difficult.

Along the northern and southern edges of the Callunetum, a vigorous growth almost entirely made up of *Carex inflata* is associated with *Sphagnum recurvum*; a 1 m. quadrat recorded in this zone (Fig. 3) is shown in Fig. 9. Here, as in many other parts of the Sphagnetum, the vegetation forms an unstable surface layer which quakes when crossed on foot. In the extensive

Sphagnetum at the western end of the Mire *Carex Goodenowii* is more abundant, while the growth of *C. inflata* is much less vigorous. *Eriophorum angustifolium* frequently plays an important part in the vegetation here, often dominating the wetter hollows where it is usually associated with *Sphagnum cuspidatum*.

The following species were recorded in this part of the Sphagnetum:

(ii) *Sphagnetum with Carices.*

<i>Sphagnum recurvum</i>	co-d.	<i>Deschampsia flexuosa</i>	r.
<i>S. cuspidatum</i>	l.co-d.	<i>Galium uliginosum</i>	r.
<i>Carex inflata</i>	l.co-d.	<i>Holcus lanatus</i>	o.
<i>Eriophorum angustifolium</i>	l.co-d.	<i>Hypnum cuspidatum</i>	l.
<i>Agrostis</i> sp.	r.	<i>H. dendroides</i>	l.
<i>Calluna vulgaris</i>	r.	<i>Juncus communis</i> (agg.)	v.r.
<i>Caltha palustris</i>	v.r.	<i>Luzula campestris</i>	r.
<i>Cardamine amara</i>	r.	<i>Menyanthes trifoliata</i>	r.
<i>Carex Goodenowii</i>	l.a.	<i>Narthecium ossifragum</i>	r.
<i>C. echinata</i>	o.	<i>Potentilla erecta</i>	o.
<i>Cladonia</i> sp.	r.	<i>Polytrichum</i> sp.	o.-la.
<i>Comarum palustre</i>	o.	<i>Ranunculus Flammula</i>	r.
<i>Epilobium palustris</i>	o.	<i>Sphagnum papillosum</i>	f.-la.
<i>Erica Tetralix</i>	l.	<i>S. rubellum</i>	f.-la.
<i>Eriophorum vaginatum</i>	l.a.	<i>Viola palustris</i>	f.

Tussocks of *Eriophorum vaginatum* are scattered throughout the Sphagnetum, and often give rise to a distinctive zone marking the transition from the Sphagnetum to the Callunetum. This transitional zone is most extensively developed at the western end of the Mire. Here there is every graduation between small isolated tussocks of *E. vaginatum* and larger composite islands several square metres in area from which the growth of the Sphagna is almost entirely excluded. The smaller tussocks are unstable and can be readily uprooted from the underlying fresh *Sphagnum* peat, whereas the islands are much firmer and often carry a stunted growth of *Calluna*, together with several species not otherwise associated with the Sphagnetum:

(iii) *Plants associated with tussocks of Eriophorum vaginatum in the Sphagnetum.*

<i>Calluna vulgaris</i>	l.a.	<i>Hypnum cupressiforme</i>	r.
<i>Deschampsia flexuosa</i>	f.	(var. <i>ericetorum</i> )	
<i>Empetrum nigrum</i>	r.	<i>Juncus communis</i> (agg.)	o.-l.
<i>Erica Tetralix</i>	l.f.	<i>Polytrichum</i> spp.	r.-o.
<i>Galium saxatile</i>	r.	<i>Viola palustris</i>	r.-o.
<i>Holcus lanatus</i>	r.		

The character of the surface and the distribution of the constituent plants are shown in a 5 m. quadrat and a transect of 20 m. recorded in the Sphagnetum of the western end of Mire (Figs. 10, 11). The vertical distribution of the Sphagna in relation to the water level is shown by the levelled bisects. *Sphagnum cuspidatum* is partially submerged, *S. recurvum* slightly above water level and above this again *S. papillosum* and *S. rubellum* in that order. Although

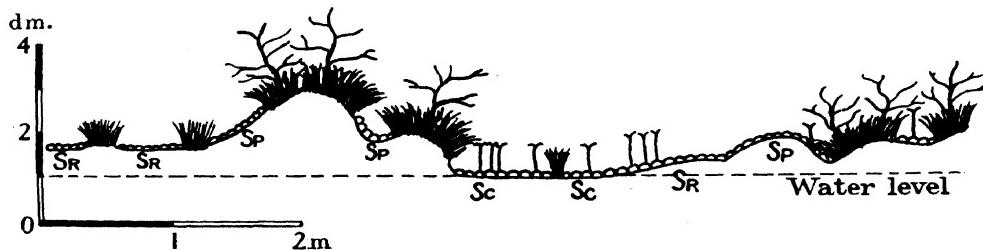
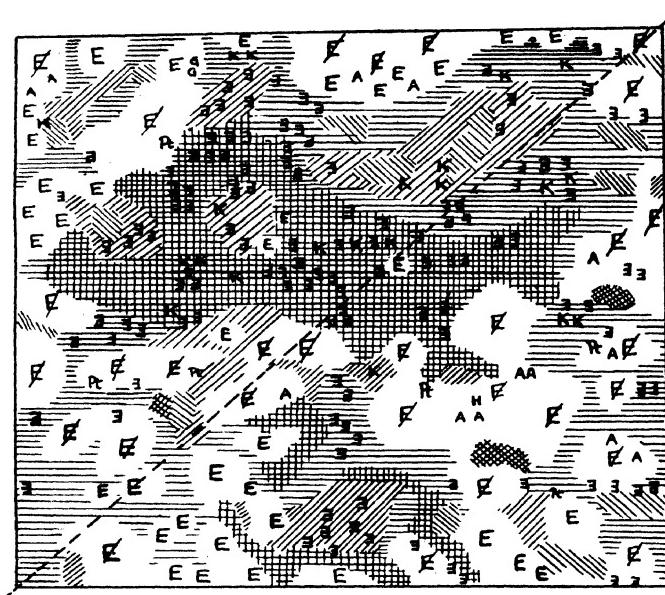


Fig. 10. A 5 m. quadrat and levelled section recorded in the Sphagnum at the western end of the Mire (position E on map, p. 21). The vertical scale of the section is  $4 \times$  horizontal.

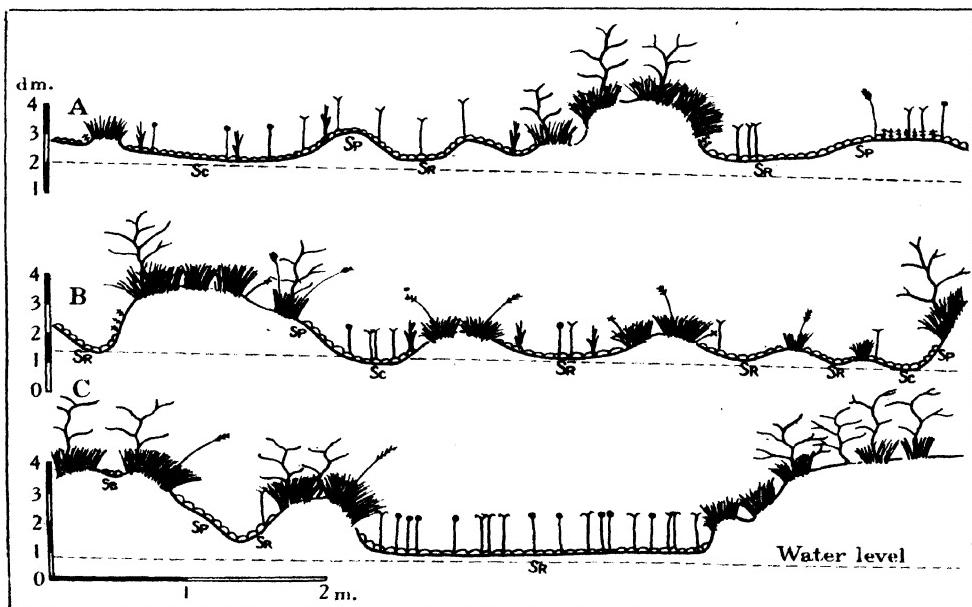


Fig. 11. A levelled transect (20 m.) passing from the Sphagnum to the Callunetum (position F on map, p. 21). The vertical scale is  $2\frac{1}{2} \times$  horizontal. Key to symbols on p. 56.

the two last-named species occupy a considerable part of the surface (see Fig. 11) they are not active in peat formation, but occupy a zone, raised by other plant remains, above the water level. *S. cuspidatum* and *S. recurvum* are undoubtedly the two mosses most active in peat formation under present conditions.

Along the sides of the Callunetum the transition to the Sphagnetum is more abrupt, although in many places a narrow zone 1–10 m. wide can be distinguished, characterized by small growing tussocks of *Eriophorum vaginatum* not overshadowed by *Calluna*. Here the growth of *Sphagnum* is confined to the intervening pools and hollows which are commonly occupied by submerged *S. cuspidatum* and a sparse growth of *Eriophorum angustifolium*.

#### D. Callunetum

A conspicuous feature of the Callunetum is the broken and uneven nature of the surface: irregular steep-sided hummocks often over 0·5 m. high are overgrown with *Calluna vulgaris*, while the intervening hollows and pools support a more varied vegetation. The only other prominent plant of the hummocks, beside the dominant, is *Eriophorum vaginatum*, which sometimes forms actively growing hummocks where the shading of the *Calluna* is not dense. There is abundant evidence that the tussocks of *Eriophorum* are frequently colonized and overshadowed by *Calluna*.

The following species were recorded growing on the hummocks in various parts of the Callunetum:

<i>Calluna vulgaris</i>	d.	<i>Hypnum cupressiforme</i> var. <i>ericetorum</i>	r.
<i>Eriophorum vaginatum</i>	l.co-d.		
<i>Cladonia</i> spp.	a.	<i>Juncus squarrosus</i>	r.-o.
<i>Dicranum scoparium</i>	f.-l.a.	<i>Polytrichum</i> spp.	o.
<i>Empetrum nigrum</i>	o.-l.f.	<i>Potentilla erecta</i>	o.
<i>Erica Tetralix</i>	o.-l.f.	<i>Sphagnum cymbifolium</i> (agg.)	l.a.
<i>Eriophorum angustifolium</i>	r.	<i>S. recurvum</i>	r.
<i>Deschampsia flexuosa</i>	o.l.	<i>S. rubellum</i>	l.a.
<i>Galium saxatile</i>	r.	<i>Vaccinium Myrtillus</i>	o.-l.f.

The vegetation of the hollows shows every graduation from a stable plant cover dominated by *Eriophorum vaginatum* and *Calluna* to the aquatic vegetation of open pools of water. A comparison of the structure of the hollows indicates that the varied vegetation may be readily interpreted as successive phases of a development in which Sphagna play an important part at first, and are later superseded by tussocks of *Eriophorum vaginatum* and *Calluna vulgaris*.

Open pools are usually rounded or oval in shape, the water being 0·5–1·6 m. in depth, with a soft peaty bottom. They are isolated from one another, and there is no evidence that they play an important part in the drainage of the Callunetum by direct surface flow of water. Overhanging shoots of *Calluna* cast a deep shade over the steep edges of the pools, and these edges are usually of bare peat with the exception of occasional mosses near to the water level.

The initial colonization of the open water takes the form of a narrow zone of submerged *Sphagnum cuspidatum*, which is frequently maintained near to the surface on the shoots of *Calluna* dipping into the water. Later, *Sphagnum cuspidatum* forms a continuous submerged layer and usually supports a sparse growth of *Eriophorum angustifolium* which helps to bind and stabilize the moss. From the first it is apparent that the colonization of the pools is limited to the open central part: a marginal zone round the edges remains where the dense shading of the overhanging *Calluna* prevents the development of the *Sphagnum* and here open water persists.

At a later stage the hollows are overgrown with *S. recurvum* which is usually maintained with its growing shoots a few centimetres above water level. *Eriophorum angustifolium* is still the only other conspicuous component of the vegetation, while *Sphagnum cuspidatum* is limited to the edges bordering the zone of open water. In this condition the vegetation forms a more stable floating platform, although it may readily be compressed and submerged by standing on it. Owing to their treacherous nature many of the open and *Sphagnum*-filled pools have been fenced, in order to prevent the loss of stray sheep.

In a few of the hollows the level of the vegetation has been further raised by the growth of other Sphagna—*S. papillosum* and *S. rubellum*—but it is far commoner to find young tussocks of *Eriophorum vaginatum* colonizing the *Sphagnum recurvum*: every stage is represented from a few scattered tussocks to an almost continuous covering of this plant to the exclusion of active Sphagna. The surface of the hollow at this phase is much more stable: it may be crossed safely on foot, and, especially when overgrown with *Eriophorum vaginatum*, only quakes slightly when jumped upon.

*Calluna vulgaris*, rooted in the raised *Eriophorum* tussocks, is a conspicuous component of the vegetation of many of the more stable hollows, and there is little doubt that this represents a later stage of the succession. The growth of the *Calluna* is usually less luxuriant and it flowers less freely as compared with that of the raised hummocks, while growing tussocks of *Eriophorum* are more abundant. The hollows are now more irregular and open in character, but many of their original features can still be recognized. Open water frequently persists in the form of treacherous crevices at the edges of the hummocks completely overshadowed by *Calluna*. It is probable that the change in the

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#### Legends to Figs. 12A-D

Fig. 12. Four quadrats with levelled sections showing the vegetation of the hollows. *Calluna* is dominant on all the hummocks and is omitted from the quadrats. Symbols as previously. A. A pool with a central zone of floating *Sphagnum cuspidatum*, supported on overhanging *Calluna* (position G on map p. 21). B. A continuous cover of *Sphagnum cuspidatum* colonized by *Eriophorum angustifolium* (position H on map, p. 21). C. A raised moss cushion of *Sphagnum recurvum* (position H map, p. 21). D. Hollows colonized by *Eriophorum vaginatum* tussocks (position J on map, p. 21).

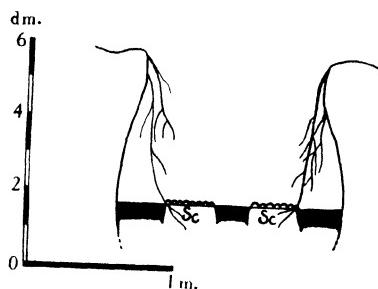
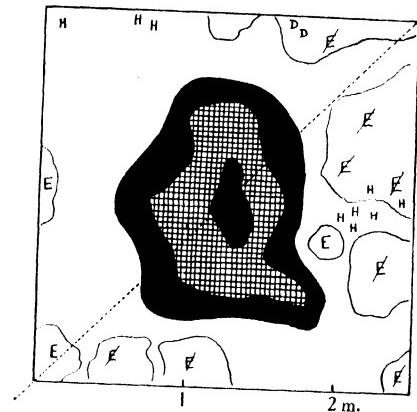


Fig. 12A.

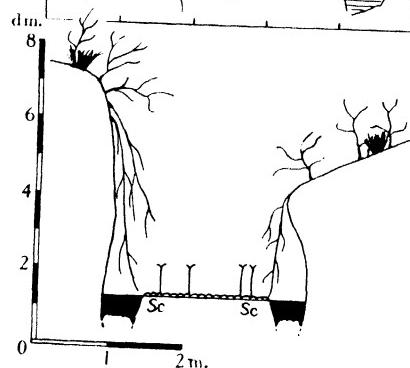
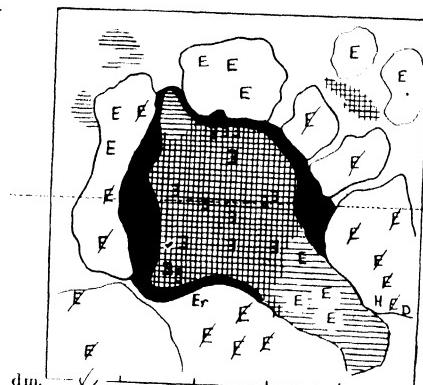


Fig. 12B.

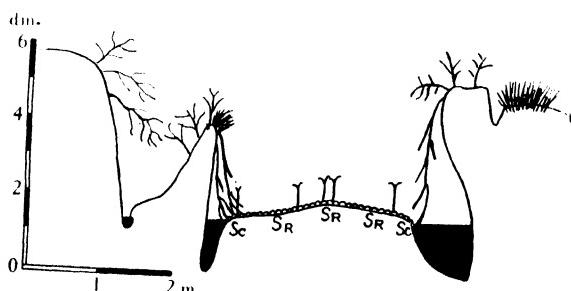
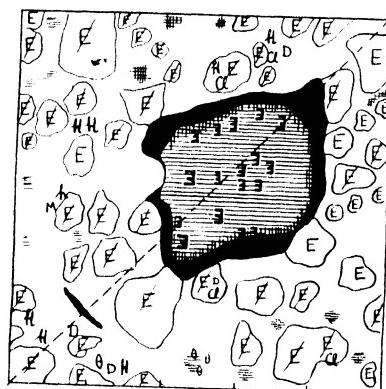


Fig. 12C.

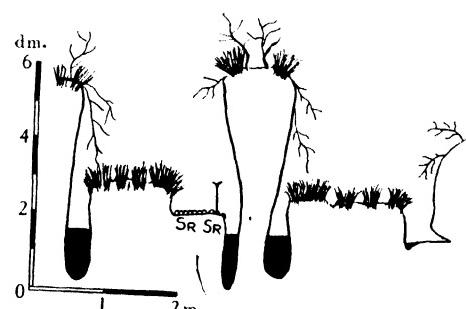
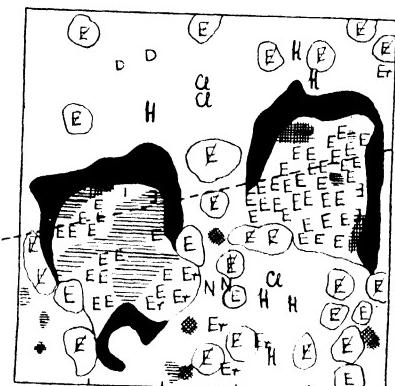


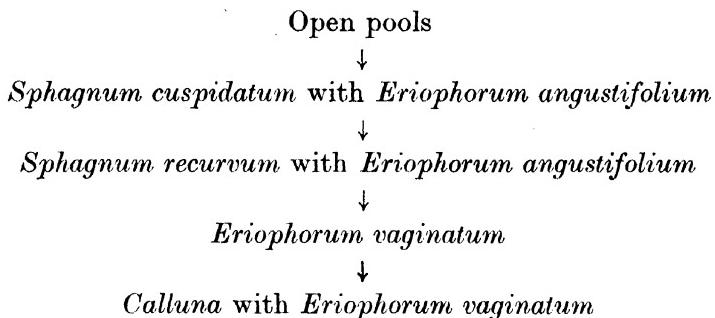
Fig. 12D.

character of the hollow arises mainly from the erosion and collapse of the hummocks. As evidenced by the steep and often undercut sides of the pools, erosion is most active near the water level. This leads to the collapse of the hummock sides with a partial filling of the narrow zone of open water; the very broken nature of the Callunetum may be attributed in large part to the gradual breakdown of the edges of the main hummocks.

Several of the stages in the colonization of the pools and hollows are shown in a series of quadrats and levelled bisects reproduced in Figs. 12 A-D. A general list of the subsidiary species found at various stages is given below:

<i>Carex spp.</i>	r.	<i>Narthecium ossifragum</i>	o.l.
<i>Cladonia spp.</i>	r.	<i>Potentilla erecta</i>	o.
<i>Empetrum nigrum</i>	o.	<i>Polytrichum spp.</i>	o.-l.a.
<i>Juncus communis</i>	o.l.		

The structure of the vegetation within the pools and hollows of the Callunetum strongly suggests that development here may be summarized as follows:



This interpretation is confirmed by the nature of the superficial peat deposits associated with the hollows. Careful excavation by digging or by hand has shown that the drier *Eriophorum* tussocks supporting *Calluna* are rooted in fresh *Sphagnum* peat in which numerous leaf bases of *Eriophorum angustifolium* are the only other recognizable remains. Similarly, underneath the surface of the pools overgrown with *Sphagnum recurvum* it is possible to detect the presence of other partially decomposed Sphagna, closely resembling *S. cuspidatum*.

The different transects across the Callunetum have shown that on passing eastwards down the Mire there is a change in the structure of the vegetation which is especially apparent in the pools and hollows. In the western and central part, the hollows are predominantly occupied by open or *Sphagnum*-filled pools, whereas at the eastern end they are nearly always overgrown with *Eriophorum vaginatum* tussocks and *Calluna*. Associated with the change in the vegetation there is evidence that the difference in level between the raised hummocks and the hollows decreases in the eastern part of the Callunetum, suggesting that in this region the level of the hollows may have been raised

slightly by the development of the vegetation. Data derived mainly from the longitudinal transect are summarized in Fig. 13 in order to show the distribution of open or *Sphagnum*-filled pools as compared with hollows overgrown with *Eriophorum* tussocks, and *Calluna*, together with the relative heights of the hummocks and hollows determined by levelling.

The mean height of the hummocks reaches a maximum value in the centre of the Callunetum. There is a considerable decrease in height at the eastern end, closely correlated with the change in the structure of the vegetation, and

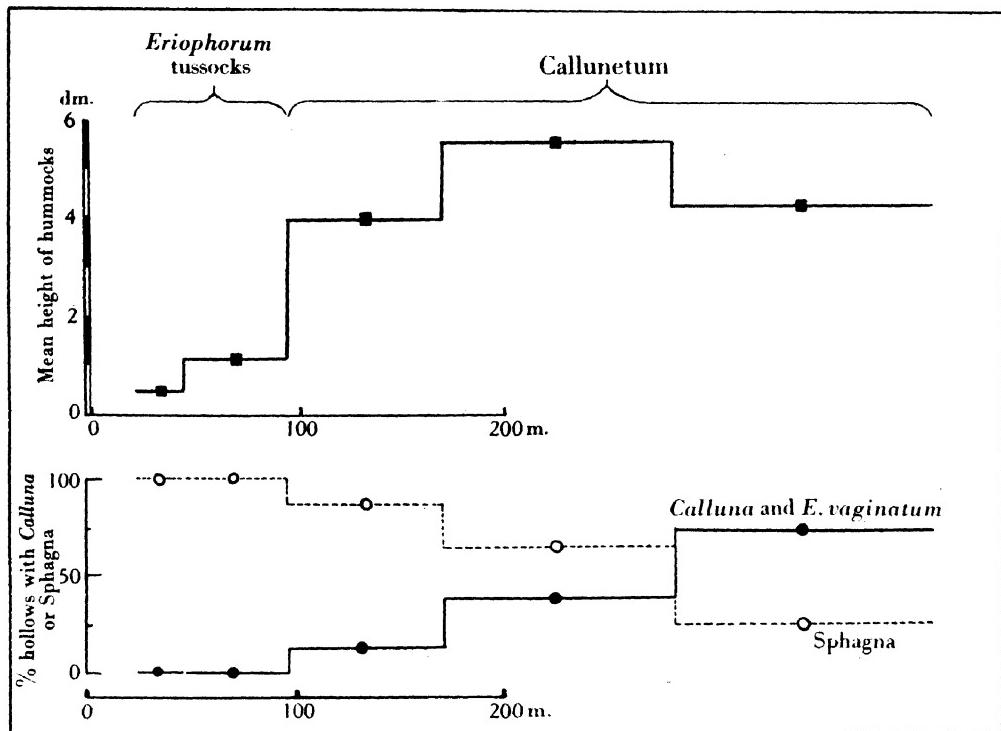


Fig. 13. The changes in the structure of the vegetation and height of the hummocks passing W. → E. down the Callunetum. Data obtained from the longitudinal transect from the centre of the Mire.

may be ascribed in part to the development of *Eriophorum* tussocks in the hollows; other contributory factors such as erosion and change in water level may have operated and will be more fully discussed. In general therefore the eastern end of the Callunetum is regarded as of more mature structure, since here the natural development of the vegetation has progressed most fully.

At the western end of the Callunetum the lower mean height of the hummocks cannot be attributed to similar causes, since here the steep-sided hollows are predominantly occupied by open or *Sphagnum*-filled pools. It is clear that the smaller hummocks in this part form a transition to the extensive *Eriophorum* islands developed in the neighbouring Sphagnetum. A fuller dis-

cussion of the successional significance of this transition will be more appropriate later.

Along the northern and southern margins of the Callunetum there are occasional hummocks, often 5–10 sq. m. in area, which are overgrown with *Calluna* but are quite isolated from the central Callunetum: they usually occur in the Sphagnetum, although several stand out as islands in the *Juncus* swamp. Both in structure and vegetation these large hummocks are clearly distinct from the *Eriophorum* tussocks of the zone of transition from Sphagnetum to Callunetum. *Juncus communis* (agg.) frequently occurs rooted at the edges, but otherwise the dense mature growth of the *Calluna* excludes practically all other species. Although mature, the *Calluna* does not flower freely, and there are indications that many of these hummocks are breaking down owing to active erosion.

#### E. Peat cuttings

The peat cuttings, like the Callunetum, present two contrasted habitats, the drier raised banks and the excavated hollows and pools. It is probable that the drier banks represent approximately the original height of the peat surface, the present levels suggesting that about 0·6 m. of the surface peat above water level has been removed from small areas both at the western and eastern ends of the channel. The dry banks of the cuttings are dominated by a rough turf, in which the following species occur:

<i>Eriophorum vaginatum</i>	I.d.	<i>Anthoxanthum odoratum</i>	O.-l.f.
<i>Nardus stricta</i>	I.d.	<i>Calluna vulgaris</i>	I.a.
<i>Deschampsia flexuosa</i>	I.d.	<i>Luzula campestris</i>	r.-o.
<i>Holcus lanatus</i>	f.-l.co-d.	<i>Potentilla erecta</i>	I.f.
<i>Juncus squarrosum</i>	f.-l.co-d.	<i>Vaccinium Myrtillus</i>	I.

The difference between the vegetation of the raised banks and the hummocks may be largely owing to their accessibility to grazing by sheep and rabbits. All the peat cuttings are situated near the margin of the Mire, and there is clear evidence that the turf is regularly grazed. Especially at the western end, shoots of *Calluna* only a few centimetres high are locally abundant, indicating the potentiality for further development of the vegetation.

In the excavated hollows the vegetation is in many respects similar to that of certain parts of the Sphagnetum. *Sphagna*, chiefly *S. recurvum*, form a continuous ground layer, associated with *Eriophorum angustifolium* and *Carices*; occasional tussocks of *Eriophorum vaginatum* occur in the older cuttings at the eastern end. The following species were recorded in these hollows:

<i>Sphagnum recurvum</i>	I.co-d.	<i>Juncus communis</i> (agg.)	I.a.
<i>Eriophorum angustifolium</i>	I.s.d.	<i>Potentilla erecta</i>	I.f.
<i>Carex inflata</i>	I.	<i>Polytrichum</i> sp.	I.a.
<i>C. Goodenowii</i>	I.	<i>Sphagnum cymbifolium</i> (agg.)	I.a.
<i>Carex</i> sp.	r.	<i>Valeriana dioica</i>	r.
<i>Eriophorum vaginatum</i>	o.	<i>Viola palustris</i>	r.
<i>Hylocomium squarrosum</i>	r.		

Although the vegetation of the peat cuttings is not of primary interest, certain points, including the effect of the removal of peat upon other communities, need consideration especially in relation to the hydrography of the Mire.

### V. HYDROGRAPHY

It is clear that the direction and extent of the surface drainage has an important influence on the spatial distribution of the main plant communities of the Mire. In this section, observations are recorded which are relevant to a more exact assessment of the effect of drainage and water level in controlling the development of the present vegetation.

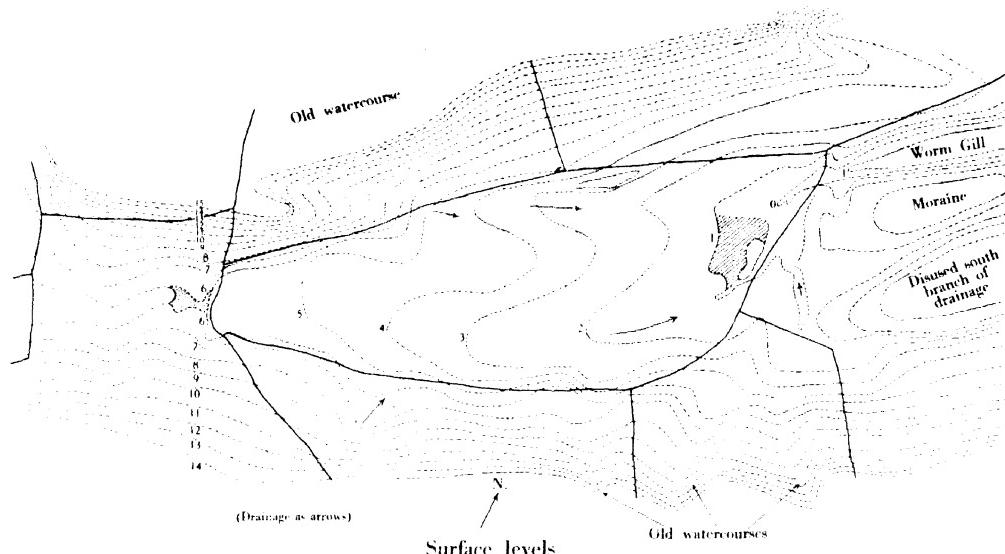


Fig. 14. A contour map of the peat surface and surrounding slopes constructed from levelled points along the transects shown in Fig. 3 together with contours from the 6 in. Ordnance Survey Map. Zero contour is 1250 ft. o.p., determined by reference to B.M. 1266. 5 ft. o.p. shown in Fig. 3. The contours (dotted lines) are drawn at 1 m. intervals, and the surrounding walls are shown as solid black lines.

#### A. Surface levels

The records of surface level are summarized as a contour map in Fig. 14, and this, used in conjunction with Figs. 1, 2 and 3, gives a clear idea of the general and detailed topography of the Mire. The U-shaped valley runs from west to east sloping gently at a fairly uniform angle of 1 in 97. The steep contours of the sides have been modified in some parts by drainage, either contemporary with or subsequent to the cutting of the channel. The section of the valley at the western end is narrow and simple, whereas that of the eastern end is wide and complicated by a band of morainic material lying longitudinally in the mouth. Survey lines running N. → S. have shown that the valley floor is not quite flat, for there is a ridge of peat which runs from a point on the north side (T. VIII, Fig. 3) eastwards down the channel. This raised

band corresponds with the Callunetum: its maximum height is the height of the raised hummocks, and this has been used in the construction of the contours. On the other hand, the levels in the hollows in the Callunetum, which were also recorded instrumentally, may be raised little above that of the general surface. The marginal channels which are parallel to the Callunetum contain the swamp communities of *Juncus acutiflorus* and *Sphagnum*. The surface is more even at the western end of the Mire where the extensive Sphagnetum and ill-defined swamp communities occupy the surface.

The areas in which peat cutting has occurred are shaded in the map, and from the levels of isolated peat banks the previous run of the contours may be estimated. The surface altered is of small area, and the cutting of peat has not affected the main run of the drainage.

#### B. *Drainage and water levels*

The affluent drainage of the Mire is derived from the adjacent limestone slopes of Stake Fell and Addleborough. During wet periods a considerable volume of water enters the Mire by seepage and surface flow, aided locally by artificial channels and drains cut in the lower slopes. The positions at which drainage enters were determined instrumentally after a period of rain in 1936 and are shown by arrows on the map (Fig. 14), an indication of the relative volume being given by the size of the arrows.

Stake Fell is by far the most important source of water entering the Mire; seven separate lines of drainage can be recognized on the southern side. The last of these at the eastern end, which joins the stream just before it leaves the Mire, has probably been opened artificially, but owing to its position has very little effect on water levels and drainage in the main part of the channel. From the slopes of Addleborough only three small streams flow into the Mire. The first of these (D) passes across the Mire and part of it joins the drainage flowing down the southern side of the Callunetum. From its special position and direction it is probable that this drainage has an important influence on water movement and water levels in some parts of the Callunetum. It is noteworthy that there is little direct surface flow of water into the channel at the extreme western end; general seepage down the adjacent slopes forms the only source of drainage water in this part. This feature of the drainage is of interest in relation to the special character of the peat deposits here.

The drainage leaving the Mire passes down Worm Gill in a natural meandering stream bed usually 2–3 m. wide, and in wet seasons it carries a rapid flow of water. The changes in the structure of the stream when traced back into the Mire strongly suggest that the effluent drainage is at present in an active state of development.

In the central parts of the Mire the position of most active drainage is marked by the *Juncus* swamp, extensively developed along the south margin under the influence of the combined drainage from Stake Fell. In this zone in

summer the water is 2-4 dm. deep, and, impeded by a floating mat of *Juncus* rhizomes, the flow is extremely slow. No well-defined banks limit the course of the stream here, but it is probable that some erosion occurs as suggested both by the unstable semi-liquid nature of the peat surface and by the high content of black organic matter carried in the water. There is no evidence of the accumulation of fresh peat under these conditions. Passing eastwards along the drainage of the south margin, the zone of typical *Juncus* swamp becomes narrower and the bed of the channel, though still overgrown with *J. acutiflorus*, is considerably lower than the banks. Near the point at which

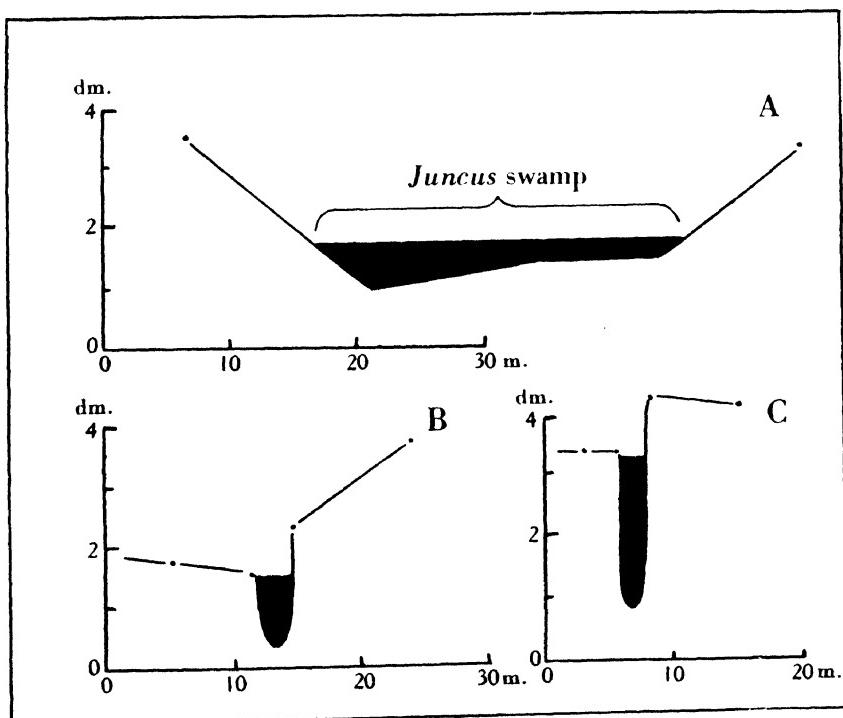


Fig. 15.

the direction of flow turns northwards, stable peat banks restrict the meandering course of the stream, and here the flow, no longer held up by *J. acutiflorus*, becomes more rapid. Farther down stream the water flows between peat banks and over rock and clay which form the floor underlying the peat deposits of the Mire. In this region it is probable that the inner peat banks have been locally destroyed by peat cutting; the beds of growing Sphagna which occupy the abandoned hollows extend almost up to the edge of the stream. These changes in the structure of the effluent drainage system are shown in a series of profiles obtained from surface levelling and boring along T. IX and the longitudinal transect (Fig. 15). The predominant influence of

the drainage from Stake Fell is apparent in the development of the present drainage system from the south side of the channel. There is no extensive *Juncus* swamp along the northern margin and no well-defined stream develops here.

Observations by means of test holes and open water during the seasons 1937 and 1938, showed that the water table through the Mire has a fairly uniform downward slope from west to east; over the total length of the Mire there is a fall in water level which is approximately parallel to the general fall in surface level. This fall in water level is clearly shown in the levelled transect reproduced in Fig. 11. Measurements of water level in a series of test holes passing from south to north across the Mire on the levelled T. X indicate that the water table in the central Callunetum may be maintained at a slightly higher level than that of the adjacent zones of Juncetum (Fig. 16 A).

From 29 August to 1 September 1938, a series of observations was made on the change in water level in different parts of the Mire. The value of these observations is enhanced by the fact that they show the effect of high rainfall followed by a period of drier weather; the first measurements were taken after a week of intermittent rain ending in a heavy downpour lasting 24 hr., while the succeeding days were cloudy but rainless. The fluctuations of water level along the transect which are summarized in Fig. 16 B illustrate the complexity of water movements in the valley. The continuous rise of water table, throughout the dry period, in the basal slopes of the south side (station 1), may be contrasted with the fall in the slopes of the north side (station 13); this makes it clear how effectively the Stake Fell catchment area dominates the water supply to the Mire. The lateral drainage channel along the south side is sufficient to carry away this influx and remains approximately constant in level. Movement of water within the Callunetum at point 8 (Fig. 16 B) is indicated by a rise of about 0.8 dm. during the period, and suggests a seepage of water longitudinally (through the peat) in the centre of the Mire. The origin of this may well be the stream running from Addleborough and flowing across the western end of the Mire. The existence of a movement of this kind is further suggested by the presence of variable water levels in the pools in the Callunetum. Within an area of 250 sq. m. the water levels in ten pools were estimated instrumentally; of these the four most westerly had water tables between 1.20 and 3.15 dm. below an arbitrary zero, whilst the more easterly six had water tables between 4.0 and 7.2 dm. below the same zero level. The slope of the water table as indicated by the levels in these holes is greater than the general slope of the surface level of the peat and so enhances the suggestion that seepage of water longitudinally in the Callunetum may take place. An inspection of the peat and vegetation of the tops of the hummocks shows that a surface flow of water at any time of year is improbable.

The evidence obtained from these measurements of water level make the conclusion inevitable that the Callunetum is not entirely ombrogenous,

although it maintains a higher water level than the adjacent communities of the drainage channels. The pools are fed in part by waters which are of re-

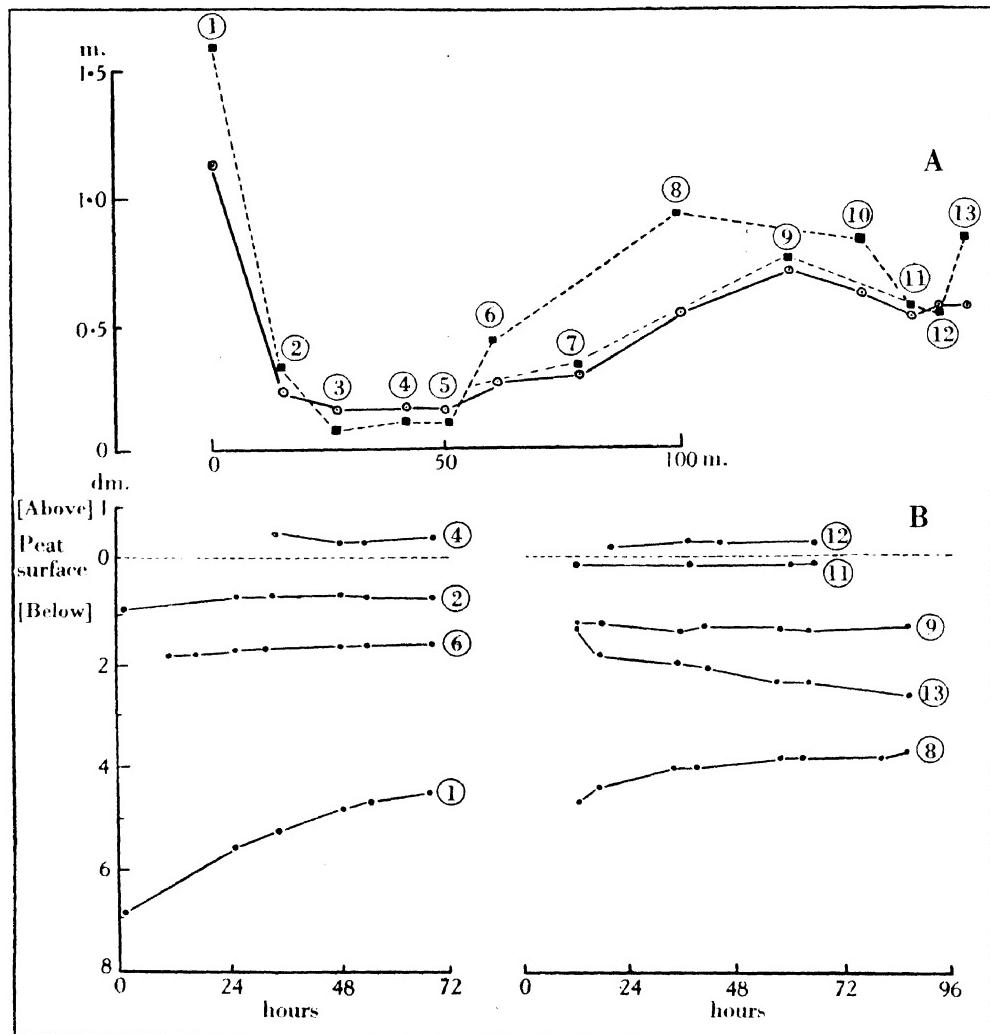


Fig. 16. A. Levels of water (solid line) and peat surface (broken line) across the Mire at T. X.  
B. Changes of water level at different stations during the period of measurement (for explanation see text).

latively high base content as indicated by estimations of  $pH$  and calcium content.

*C. Acidity and calcium content of water and peat*

The following table gives the values of pH and calcium content of water in various plant communities of the Mire:

	Sphagnetum with			
	Juncetum	<i>J. acutiflorus</i>	<i>Carex</i> and <i>Eriophorum</i>	Callunetum pools
pH: range	6.7-7.6	6.2-6.8	5.0-6.6	6.2-6.5
mean	7.1	6.6	6.2	6.3
Ca mg. per 100 c.c.: range	6.5	8.0	3.8-6.6	4.4-6.5
mean			5.1	5.7

From these figures there can be little doubt that the water in all the communities is slightly acid to neutral, while the calcium content indicates that it is of relatively high base status. These figures help to explain the relatively great importance of *Sphagnum recurvum* in the actively regenerating zone.

Figures for the pH of the peat in various communities are given in the table below:

Community	Grassland of the slopes	Callunetum of the slopes	Juncetum acutiflori	Sphagnetum		Callunetum
				<i>J. acutiflorus</i>	<i>Carex</i>	
pH: range	4.7-5.9	4.3-4.5	6.0	4.8	4.7	3.7-4.8
mean	5.3	4.4	6.0	4.8	4.7	4.4

All these peat substrata with the exception of that of the Juncetum acutiflori are subject to some drying and oxidation during the year. The higher acidities of the peat than the water may be explained as due to leaching and the production of acid during oxidative breakdown of plant debris.

**VI. PEAT DEPOSITS AND STRATIGRAPHY**

The limestone rock of the channel floor is covered to a variable depth by a deposit of clay ranging in colour from deep blue to light greyish blue. The clay often contains a considerable quantity of large limestone fragments and pockets of coarser sandy material, the latter presumably derived from the decay of limestone in situ. It is probable that the clay was deposited from water during a late stage in the use of the channel in the glacial drainage system, and has been to some extent modified and redistributed by subsequent local drainage. The existence of the relatively impervious clay layer may be of general significance in that it prevented the escape of water by underground drainage systems which are common in the vicinity.

From the many borings in which the depth of the peat has been recorded it has been possible to reconstruct with reasonable accuracy the level of the underlying deposit. Such a reconstruction is of interest since it gives an

indication of the primitive structure of the channel floor preceding the accumulation of peat. The results are summarized in the contour map (Fig. 17). A comparison of this map of floor levels with the preceding contour map of surface levels of peat at once shows the manner in which peat accumulation has influenced the slope of the channel. The present peat surface falls eastwards with a gradient of 1 in 97, whereas the channel floor had a gradient of only 1 in 145 as calculated over the total length. Moreover, the original floor increased in slope passing westwards towards the watershed, while this condition of the surface has been partly reversed by the accumulation of peat. The thickest peat deposits lie in the centre of the Mire over the deeply excavated channel, while eastwards and towards the margins there is a rapid decrease in thickness.

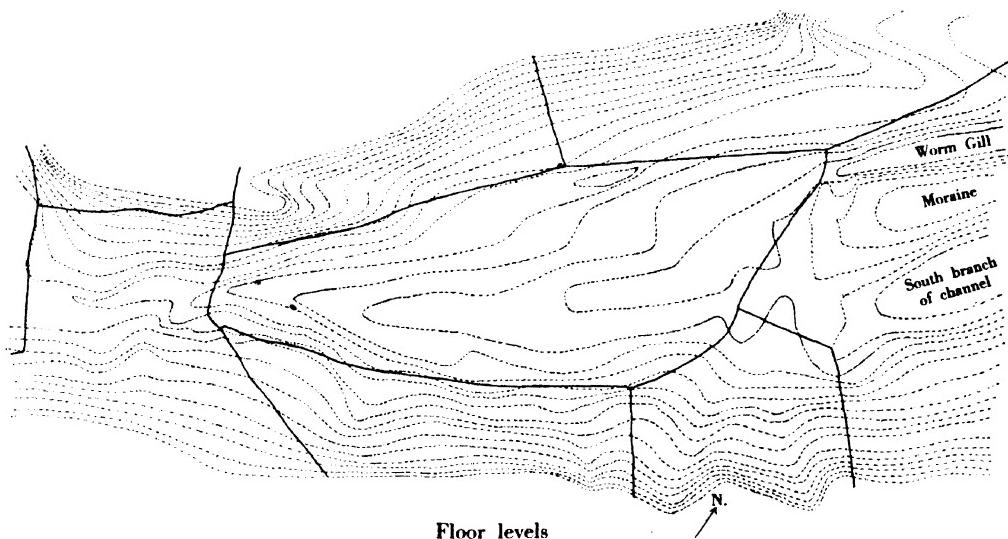


Fig. 17. A contour map of floor levels derived from the borings along the levelled transects shown in Fig. 3. The contours (dotted lines) are drawn at 1 m. intervals, zero being 1250 ft. o.d., and the surrounding walls are shown as solid lines.

Two distinct types of peat, differing in the nature of their constituent plant remains, are widely distributed in the Mire. The first of these is characterized by the abundance of the remains of more eutrophic plants, such as *Phragmites*, *Juncus* and *Equisetum*, and it usually contains a considerable quantity of well-preserved wood. At all positions investigated by digging or boring, peat of this 'fen' type forms a lower layer of variable thickness overlying the clay deposit of the channel floor. The second type of peat is distinguished by the predominance of the remains of more oligotrophic plants, viz. *Sphagna*, *Eriophorum* and *Calluna*. This acidic peat forms the upper and superficial layers of the deposit in the central parts of the Mire. The general stratigraphy of a profile exposed by digging through a raised hummock in the

central Callunetum is summarized below to show the distinctive structure of the peat deposit.

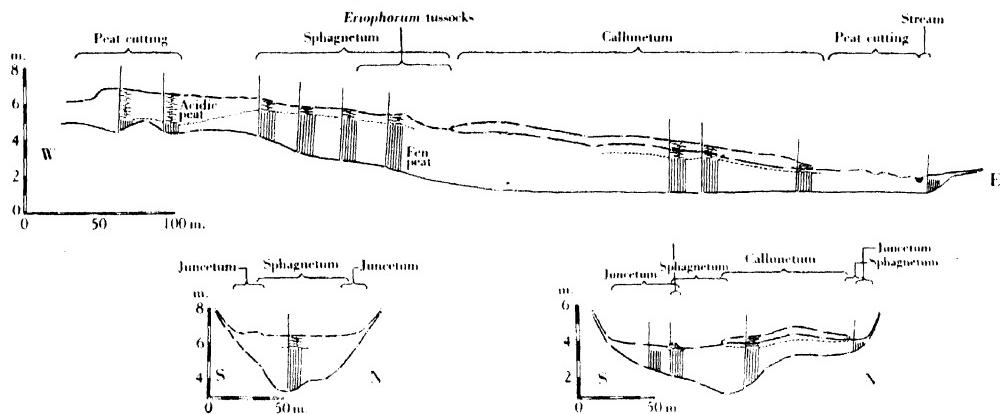
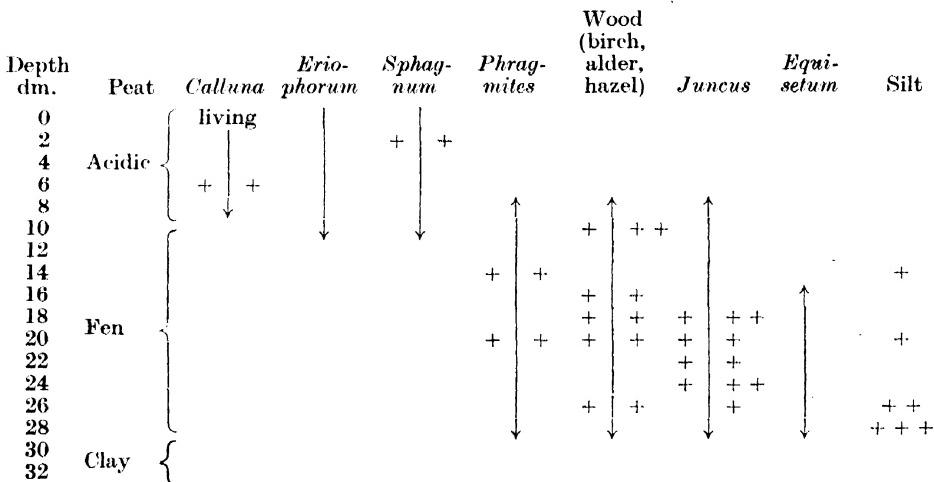


Fig. 18. The distribution of acidic and fen peat determined by boring and digging along the levelled longitudinal transects and T. VII and T. IX.

Acidic peat

Fen peat

The general distribution of acidic and fen peat in the Mire is indicated by the borings and diggings along a longitudinal section and two transects (T. VIII and T. IX) summarized in Fig. 18. It is clear that the greatest accumulation of acidic peat has occurred at the western end of the Mire. Here the fen peat forms a relatively thin zone above the blue clay, and although it contains well-preserved remains of *Phragmites* rhizomes it is almost devoid of wood, in contrast to the fen peat of other regions. The overlying acidic peat in this part is made up almost entirely of partially humified and compact *Sphagnum*, containing very few remains of *Eriophorum* and *Calluna* which are important constituents of the acidic peat elsewhere.

Farther eastwards in the Sphagnetum the fen peat is much thicker, and abundant wood remains were recorded from all the borings. Fresh uncompacted *Sphagnum* peat saturated in water is the chief constituent of the upper layers, which also contain numerous leaf bases probably of *Eriophorum angustifolium* and *Carices*.

In the Callunetum the structure of the acidic peat is much more complex. The hollows, as already indicated, are filled mainly with fresh *Sphagnum* peat, clearly distinct from the more humified black-brown peat of the raised hummocks, in which can be recognized the remains of *Sphagna*, *Eriophorum vaginatum*, *E. angustifolium* and *Calluna*. Careful excavations of the hummocks has shown that a definite relationship between the above components of the peat usually occurs. The compacted *Sphagnum* peat forms an important constituent of the hummocks, and in it are embedded the tough fibrous remains of *Eriophorum vaginatum* tussocks with which flattened debris of *Calluna* are usually associated. The more detailed stratification observed in digging through a large hummock in the centre of the Callunetum was as follows:

Depth dm.	Description
0-0.5	Black surface peat with living roots of <i>Calluna</i>
0.5-1.5	Fibrous peat of <i>Eriophorum vaginatum</i>
1.5-2.75	Light brown compact <i>Sphagnum</i> peat with <i>Eriophorum angustifolium</i>
2.75-5.5	Black fibrous peat containing <i>Eriophorum vaginatum</i> and <i>Calluna</i>
5.5-6.75	Light brown <i>Sphagnum</i> peat

The exposure of longer profiles crossing the hummocks has shown that the different layers do not form regular horizontal zones, but exist as isolated pockets, varying widely from place to place; in one digging eight zones were recognized, representing four cyclical changes from *Sphagnum* and *Eriophorum* to *Calluna*. A zone containing abundant wood and twigs, chiefly of birch, often underlies the upper acidic peat; this layer is frequently embedded in a black amorphous matrix which appears to be derived from highly humified *Sphagnum*. Below this is typical fen peat, with wood and twigs extending throughout down to the underlying clay and rock; large trunks and stools have been frequently excavated. Especially in the lower layers of the fen peat, zones of peaty clay sometimes occur: at one point at the eastern end of the Callunetum a deposit of pure silt 1 dm. in thickness was encountered in the peat at 1.1 m. above the channel floor.

In the peat deposits of the margin of the Mire there is no evidence of the accumulation of acidic peat. Borings in the region of the *Juncus* swamp indicate that the more stable peat underlying the water is made up of fen plants and contains well-preserved wood and *Phragmites* remains. The only acidic peat in these areas is associated with the isolated *Calluna* tussocks in which the remains of *Sphagnum* and *Eriophorum vaginatum* are raised above water level. Similarly, at the extreme eastern end, just beyond the stream,

traces of acidic peat are lacking: the superficial layers are here made up of 2-3 dm. of black amorphous peat overlying the fen peat.

Analyses have shown that different kinds of peat have widely different ash contents. Four samples of acidic peat taken from a hummock in the Callune-tum down to a depth of 5 dm. had a mineral ash content varying from 3·2 to 4·8% of the total dry matter with a mean of 3·7%, while the values obtained from four samples of fen peat varied from 6·5 to 13·1% with a mean of 10·4%.

## VII. DISCUSSION OF PLANT SUCCESSION AND DEVELOPMENT OF THE MIRE

The general structure of the peat deposits shows that there has been a succession of vegetation which resembles in many respects that often associated with raised-bog formation. Compared with the raised bogs which have been described in this country there are, however, certain distinctive features both in the general morphology of the Mire surface and in the plant covering. The surface has a downward slope from west to east, and the level of the central part has not been extensively raised above the margin, although incipient raising in the form of large hummocks is apparent. Moreover, in most of the central area there is at present a deposition of peat only in the hollows and pools, and the natural development of the vegetation leads to an almost continuous cover of *Calluna* with a further retardation of peat formation. In attempting to trace the sequence of changes which has led to the present condition of the Mire the influence of the following factors must be taken into account:

- (1) The development of the vegetation leading to the accumulation of peat and the consequent modification of the drainage system of the channel.
- (2) A special feature of the topography which consists of a small valley inset in a large catchment area of Yoredale limestone.
- (3) The modification of the drainage system of the catchment area; especially the disappearance of streams into underground courses and the leaching of the surface soil.
- (4) The direct and indirect effect of climatic change upon the above factors.

It is most profitable first to discuss the evidence concerning the natural succession of the vegetation and the direct influence of peat accumulation on the conditions for plant growth in the channel.

From its manner of formation it is unlikely that the channel, after its disuse as part of a glacial drainage system, ever contained any considerable sheet of open water. The reconstruction of the levels of the basal clay, Fig. 17, fully supports this conclusion. The wide floor of the southern branch of the main channel suggests that it was not eroded by local drainage, although some erosion seems to have occurred down Worm Gill which carries the present stream. Thus there is no evidence that drainage eastwards was ever sufficiently

impeded to lead to an accumulation of any considerable volume of open water in the upper parts of the channel. Shallow ponds may have covered the surface at the eastern end, although these could hardly have exceeded 1 m. in depth owing to the nature of the contours of the blue clay and rock.

The structure of the basal layers of peat indicates that, at the beginning of peat formation, the floor was colonized by semi-aquatic vegetation in which *Equisetum* was conspicuous: woody species made their appearance early, especially at the margins of the channel. Since, at this phase, peat accumulation depended on a high-water table, it seems likely from the contours of the floor that it started first at the eastern end of the Mire. This would impede the effluent drainage and tend to increase the amount of drainage water held in the channel. Under the influence of this retardation of drainage *Phragmites* and *Juncus* (an articulate species) soon spread to cover the whole channel floor. The occurrence of pure or almost pure silt in the lower layers of the peat demonstrates that at this period active drainage from the channel sides had a widespread influence upon the whole floor: the vegetation must have been subjected to flooding by base-rich water. Throughout the period of accumulation of *Phragmites* and *Juncus* peat there was a sporadic colonization of some areas by scrub in which *Betula*, *Alnus* and *Corylus* have been recognized from the remains of wood, bark or fruits. From the depth of the deposit it may be deduced that the community was relatively long-lived. It probably depended for its existence on periodic flooding of the whole area with base-rich water, whilst the preservation of plant remains resulted from permanent waterlogging of the substratum.

As the depth of the peat increased, so the angle of the slope from west to east, and consequently the rate of run-off of drainage water, also increased. These are conditions which would lend to a partial localization of drainage; for the greater the angle of slope, the greater the rate of flow of water at the margins of the Mire where the affluent drainage debouches from the hills, and the centre of the Mire becomes less directly influenced by drainage. This tendency of the drainage to become localized owing to the increase of the run-off, may be visualized as an important factor in the development of more oligotrophic vegetation in the centre of the Mire. Throughout the period of increase of slope there may have been a reduction of peat accumulation at the margins as compared with peat accumulation at the centre of the Mire. When oligotrophic vegetation became established in the centre, this effect was probably exaggerated and led to further constriction of marginal drainage. Finally, as will be shown later, there was probably a marked erosion of the marginal peat in those parts carrying the rapid flow of water.

The acidic peat of the centre of the Mire contains several layers, which indicate a succession of communities. The basal zones are highly humified but seem to consist of a matrix of *Sphagnum* peat, in which are embedded trunks and twigs of *Betula*, with local pockets of the eutrophic *Phragmites* and *Juncus*,

and the more oligotrophic *Eriophorum*. Following this there was a further colonization by oligotrophic species, while trees, *Phragmites* and *Juncus* disappeared. The main constituents of the upper peat horizons are *Sphagna*, *Eriophora*, and *Calluna*, and the stratigraphy indicates the establishment of a regenerating cycle similar to that already described in the fenland peat by Godwin & Clifford (1938). *Sphagna* are superseded by *Eriophorum* and *Calluna*, the surface being made up of a mosaic of small areas in different stages of the cycle. This was for a time a relatively stable self-regenerating community-forming peat.

As the peat increased the water table must have been maintained at a higher level, and there is little doubt that the maintenance of the water table, at or near the surface, was a master factor in determining the stability and successful development of this community. Two forces seem to have combined to bring about its degeneration to the present Callunetum. First, the growth of peat up to a critical height and slope from the marginal drainage, and secondly, the decrease in height of the marginal water level, owing to the further development by erosion of the effluent drainage from the Mire. Increasing colonization by the more xerophytic member of the communities would be expected until a stage comparable with the present dominance of *Eriophorum* and *Calluna* was attained.

The present pitted surface may have resulted from the luxuriant growth of the *Calluna* under dry conditions, the close canopy shading out subsidiary vegetation. The bare peat beneath this canopy would be subjected to rapid erosion except where stabilized by the root systems of the dominants. When the holes so formed became sufficiently wide and deep to expose unshaded water or peat surfaces to light, a subsidiary cycle arises in which hydrophytic *Sphagna* are followed at first by mesophytic species and later by *Eriophorum* and *Calluna* once more. The fall in water table in the central region is evident from the presence of *Sphagna* in the peat of the *Calluna* hummocks, at a height of about 0·5 m. above the level at which active regeneration of *Sphagnum* now occurs.

These interpretations of the course of development of the Callunetum find valuable confirmation in the distribution of existing communities in the Mire, and their relationship to water level. The most highly developed Callunetum is found at present at the eastern end of the Mire, where the holes are occupied, in the majority of cases, by stable vegetation consisting of *Eriophorum vaginatum* and *Calluna*. Proceeding westward, the holes become progressively less dominated by these plants, and more open and treacherous: *Sphagnum recurvum* and *Eriophorum angustifolium* dominate those which are more advanced, and *Sphagnum cuspidatum* and open water appear in the more primitive. The proportion of holes with open water or very loose bare peat surfaces increased greatly towards the west, until the Callunetum finally gave way to a community dominated by *Sphagnum* and containing locally at first

large, and later small, *Eriophorum* islands, which bear a stunted growth of *Calluna*. Farther westward an extensive area of high-water table (within 1 dm. of the surface) bears the Sphagnetum, in which are associated *Eriophorum angustifolium* and *Carices*. This zonation approximates in many respects to the sequence of development suggested by the peat profiles in the mature Callunetum. It is therefore of great interest to attempt to distinguish the factors leading to this east to west zonation of communities.

Clearly, the Sphagnetum is associated with a water level maintained close to the surface, whereas the mature Callunetum is associated with a water level maintained well below the surface. It is difficult to escape the conclusion that the spatial relationship of these extreme conditions and their intermediates is closely correlated with the development of drainage from the Mire. As shown already (Fig. 15, p. 41) the form of the main drainage changes in an east to west direction: the well-defined stream of the eastern end gradually changes into a wide *Juncus* swamp, and later into an ill-defined zone of swamp communities surrounding the Sphagnetum.

At the eastern end the effluent drainage has eroded a channel through the peat down to floor level, while farther back it still runs over the lower peat deposits. In this eastern area, therefore, it is probable that the water level in the drainage channel has been significantly lowered by erosion, and so decreased the water level in the neighbouring Callunetum. Farther west, where marginal drainage is not restricted to a channel, erosion is less deep, and a smaller fall in water table may have resulted. Here the water level has fallen far enough below its previous level for full colonization of hummocks by *Calluna*, whilst maintaining sufficient water in the holes for the growth of *Sphagnum*. The extent of erosion in this region may be estimated by the heights of the vertical bare sides of the hummocks of the Callunetum where they abut upon the line of drainage, i.e. about 0·3 m. At the western end of the Mire, where no erosion is obvious, the surface is dominated by a Sphagnetum in which there occur many of the features of a regeneration cycle. The extensive survival of such a community in this position alone is highly suggestive of the importance of drainage development and erosion in controlling the distribution of plants playing an active part in peat formation.

It is necessary at this point to assess the importance of peat cutting which has taken place over a restricted area at the eastern end of the Callunetum. There is sufficient evidence that it did not involve a serious modification of the main drainage system for the stream is still in a meandering bed, which shows little sign of human interference. Moreover, a bank of peat was left which maintained the stream in its original course, so that it does not flood the cuttings. It is probable that the peat was removed to a depth of about 0·6 m. as a surface layer, and the position at which this removal took place is significant, in that it represents that part of the Callunetum in which the water table would be maintained at the greatest distance from the surface, thus

making peat digging possible. The removal of peat probably accelerated the drying of the adjacent peat of the Callunetum, but from its position it is unlikely that the effect was more than local.

To sum up these points, the spatial relations of the communities may be related with two factors, which, acting together, tend to lower the water table of the central region. First, the upward growth of peat by a regenerating cycle, and secondly, the lateral erosion of the channel, which lowers the water table in the peat. These two factors must be considered as closely interrelated, and as reacting simultaneously on the ecosystem. Peat digging had merely a local accelerating effect on the lowering of the water table, since it did not change significantly the main drainage system.

The recognition of erosion as an important factor in the development of the oligotrophic vegetation of the Mire gives a consistent interpretation of several difficult features:

- (1) The general structure of the stream and swamp communities.
- (2) The presence of *Sphagnum* in the peat at about 0·5 m. above the present water level.
- (3) The abrupt rise of the central Callunetum above the lateral communities.
- (4) The east to west zonation of vegetation.
- (5) The position and even surface of the regeneration zone of the Sphagnumetum.

The disappearance of *Phragmites* from the communities of the marginal drainage is more difficult to explain. This species has been entirely superseded by *Juncus acutiflorus* which now dominates the eutrophic communities. There is no doubt, however, that the restriction of direct drainage water, to relatively narrow channels, has completely altered the habitat available to eutrophic plants. It might be suggested that the increased rate of flow of water has made it impossible for *Phragmites* to compete successfully with *Juncus acutiflorus* upon an unstable peat substratum. Further, there exists the possibility of changes in the chemical constitution of the drainage water, but this will be considered later.

The above discussion has involved a consideration of those factors arising solely out of a change in the Mire itself. It now remains to consider the possible effects of allogenic factors, in so far as they react upon the important autogenic factors.

A special feature of the topography is that the catchment area of limestone rock is large in comparison with the Mire surface, hence the drainage water entering from the hillsides is large in quantity and rich in bases. The maintenance of an eutrophic vegetation under these conditions depends solely on the maintenance of a high water table throughout the year. It is of interest that the peat at the extreme western end of the Mire, where affluent drainage is at its minimum, shows that the development of oligotrophic vegetation

could occur locally at an early stage. Owing to the absence of lateral erosion, the *Sphagnum* peat showed a more uninterrupted development here, and was not extensively colonized by *Eriophorum* or *Calluna*. The appearance of oligotrophic vegetation in the main part of the Mire has been related to factors arising from the canalization of the drainage. Nevertheless, other factors, alloegenic in origin, may have exerted an important influence. There is evidence that the volume of drainage water reaching the Mire from the catchment area may have decreased owing to the formation of subterranean watercourses in the limestone rock. The abandoned waterfalls of Stake Fell may well flow through the rocks of the basin. This is a common feature of this geological stratum, and many streams, including Worm Gill, the outgoing stream of the Mire, are lost in the rocks at some point in their courses. Coupled with this decrease in water, there may have been a change in the mineral content of the water, arising from the leaching and incipient podsolization of the surface strata of the catchment area: the vegetation of the hillsides is dominated locally by a Callunetum, clearly indicating an effect of this sort. Both of the above factors would operate to reduce the volume and mineral content of the drainage water and hence accelerate the replacement of eutrophic plant communities.

Besides these factors it is reasonable to suppose that major climatic changes may have influenced the course of development of the Mire. No exhaustive discussion of this aspect can profitably be attempted here as it must depend on a further collection of evidence, but it is clear that in so far as water level is a major factor, the effect of rainfall may very well be far-reaching. A high rainfall and plentiful supply of drainage was essential for the primary colonization and accumulation of peat. Subsequent to the development of localized marginal drainage, the effect of increasing rainfall would be more complex: it would encourage the upward development and raising of the oligotrophic communities under the influence of base-poor rain water, but the simultaneous increase in volume of drainage water would not only restrict the area of ombrogenous peat formation but also accelerate erosion. Under climatic conditions at present prevailing there is no doubt that the centre of the Mire is not completely ombrogenous. Evidence has been put forward to show that there is a movement of water by seepage down the Callunetum. This water probably has its origin in a drainage system from Addleborough (D 7, map, Fig. 14) which crosses the western end of the bog in the Sphagnetum, and to this feature may be attributed the abundance of the relatively less oligotrophic *Sphagnum*—*S. recurvum*—in both the Callunetum and the Sphagnetum; moreover, the water in both these parts is only slightly acid and contains a considerable amount of calcium.

Despite these special features of the vegetation and hydrography, the Mire bears a striking superficial resemblance to the raised bogs described by Godwin & Conway (1939, Fig. 1, p. 114), and Tansley (1939, p. 684, Fig. 138). Especially

noteworthy in this regard are the two marginal laggs continued as a more rapid outgoing stream of relatively high pH and base content. Delimited from the valley sides by these laggs is a central raised region colonized by more oligotrophic communities. At the head of the valley near the watershed there occurs a region in which *Sphagnum* and *Eriophorum* are actively forming peat: this is the position in which the regeneration complex is usually found.

The most striking points of difference between Thornton Mire and the raised bogs described are the slight elevation of the central region, so that the contours are dominated by the east to west slope of the surface, and the absence of a typical raised bog 'regeneration complex'. The regeneration cycle differs from the 'regeneration complex' of the raised bogs in the relative unimportance of oligotrophic Sphagna in peat formation, and in the abundance of *Eriophorum angustifolium*, *E. vaginatum*, and *Carices* in the Sphagnetum. The preponderant influence of drainage water in so small a valley may account for this and for the important influence of erosion.

It is probable that erosion by localized drainage is not a rare phenomenon, but may provide valuable clues to the interpretation of certain features of raised bogs which seem to us to present some difficulty. It is an important characteristic of peat deposits that the development of drainage involves erosion, not only when water flows along the margin but also when it drains from raised parts of a mire. Hence, for instance, steepness of the rand slope may result from the influence of three factors:

- (a) The accumulation of acidic peat.
- (b) The erosion of peat by drainage from the surface of the Mire.
- (c) The erosion of peat by the marginal drainage of the Mire.

It seems unlikely that the growth of the central oligotrophic communities could of itself produce an abruptly rising rand slope owing to the difficulty of maintaining a steep water table close to the surface; moreover, it involves the assumption that the retarding effect upon the peat growth of the base rich waters of the lagg is sharply restricted to the confines of the lagg itself. These two essential conditions could only, it seems, be realized where the rainfall was high and the surface soil of the catchment area podsolized. It has been observed, however, that the steepness of the rand is least under such climatic conditions, and an explanation might be found in the erosion of the rand by drainage from the Mire, leading to limitation in slope. The steepest rand slopes are found in those mires where rainfall is low, and where lateral erosion of the peat may become predominant.

Preliminary observations on Hukermire, which occupies a channel parallel to that of Thornton Mire (see map, Fig. 1), have revealed the presence of a community, resembling more closely the regeneration complex of true raised bogs. Moreover, the drainage relations of this Mire appear to be entirely different, and it is hoped that a critical comparison will allow a more accurate estimate of the influence of drainage and erosion on bog formation.

### VIII. SUMMARY

In this paper an account is given of the ecology and structure of the peat deposits of a disused glacial drainage channel in the Central Pennines at Thornton Mire, Wensleydale.

The vegetation of the surrounding slopes is briefly described, together with the structure and distribution of the main plant communities of the Mire. Quadrats and levelled bisects recorded in typical parts of the *Juncetum acutiflori*, *Sphagnetum*, and *Callunetum* are shown to illustrate the character of the vegetation.

The general morphology of the Mire surface and the distribution of peat were investigated by levelling and boring along a series of transects, and the results are summarized as contour maps.

The stratigraphy of the peat deposit shows that there has been a plant succession involving the widespread replacement of eutrophic 'fen' communities by the more oligotrophic ones which are at present active in peat formation. An attempt is made to distinguish some of the important conditions which have influenced this plant succession during the development of the Mire. Several sources of evidence indicate clearly the importance of drainage conditions and water level. It is suggested that the establishment of marginal drainage and its subsequent development by erosion may have a controlling influence on the distribution of oligotrophic plant communities and peat accumulation both in this and other peat mires.

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## KEY TO SYMBOLS OF QUADRATS AND BISECTS

	Quadrats	Bisects		Quadrats
<i>Calluna vulgaris</i>			<i>Caltha palustris</i>	C
<i>Carices</i>	K		<i>Cladonia</i> sp.	Cl
<i>Eriophorum vaginatum</i>	E		<i>Comarum palustre</i>	P
<i>E. vaginatum</i> (overgrown by <i>Calluna</i> )	E		<i>Dicranum</i> sp.	D
<i>Deschampsia flexuosa</i>	A		<i>Epilobium palustre</i>	e
<i>Narthecium ossifragum</i>	N		<i>Erica Tetralix</i>	E+
<i>Eriophorum angustifolium</i>	E		<i>Galium uliginosum</i>	G
<i>Polytrichum</i> sp.			<i>Holcus lanatus</i>	B
<i>Sphagnum cuspidatum</i>			<i>Hypnum</i> spp.	H
<i>S. recurvum</i>			<i>Mentha aquatica</i>	M
<i>S. papillosum</i>			<i>Menyanthes trifoliata</i>	Y
<i>S. rubellum</i>			<i>Myosotis</i>	F
Open water			<i>Plagiothecium undulatum</i>	Θ
<i>Agrostis</i> sp.	t		<i>Ranunculus Flammula</i>	R
<i>Anagallis tenella</i>	A		<i>Scabiosa succisa</i>	♂
			<i>Viola palustris</i>	∨

## THE VEGETATION OF THE BARNACK STONE QUARRIES

### A STUDY OF THE VEGETATION OF THE NORTHAMPTONSHIRE JURASSIC LIMESTONE

By IAN HEPBURN

(*With Plate 1 and two Figures in the Text*)

A REFERENCE in Prof. A. G. Tansley's monumental work, *The British Islands and their Vegetation*, in the chapter on the Chalk Grassland, to the fact that practically no records had been obtained for the similar vegetation on the Oolitic limestones, suggested that a study of an area on the Jurassic limestone in Northamptonshire might be of some interest.

The following account is concerned with the vegetation that occurs over the disused stone quarries at Barnack, near Stamford, which, owing to the uneven state of the ground, has not been grazed or put to any other agricultural use which might modify the natural vegetation. Practically all the grassland in the county has been completely altered by agriculture, and thus an untouched area of this type is of particular interest.

Barnack quarries were amongst the most famous in England. They were undoubtedly worked in Roman times, as witness certain carved stones found in the neighbouring parish of Castor and elsewhere. They were a source of an immense quantity of ecclesiastical building stone in Norman times and throughout the Middle Ages. The great abbeys of Peterborough, Crowland, Ramsey, St Edmundsbury, etc., all had rights to quarries in the district, and, owing to the easy transport provided by the Welland and the Nene, or via the neighbouring highway of Ermine Street, a very large number of churches in the eastern counties were built of Barnack Rag. The most famous of these are the fine marshland churches round the Wash, Norwich Cathedral, and many fine churches near the Nene and Welland valleys. The actual date of the final closing down of these quarries is difficult to ascertain, but it is generally believed that they were practically worked out by 1500.

Traces of many quarries can be seen in the parish of Barnack and in the next parish of Southorpe. The site of the largest quarry is known locally as 'The Hills and Holes', and is the subject of this study. It comprises an area of nearly 60 acres and has obtained its local name from the very irregular appearance of the grassland which has formed over the old workings and piles of waste debris. As far as can be ascertained it has never been put to any agricultural use since the quarries ceased functioning, and has not been grazed, at any rate in recent times. For years it has served as playground for the

village children, and, on occasions recently, has unfortunately been used as an exercise area for the local Tank Corps, though this has done very much less damage to the flora than was at first feared. There is no sign that the herbage has been influenced to any extent by rabbits. It has, however, been the habit to burn the grass in the autumn, though this has never been carried out systematically or regularly. It is probably due to this periodical burning that the herbage, especially on the sides of the 'hills', has remained as open as it has, so that the stronger grasses have not been able to gain control and choke out the more interesting herbs. This factor is, therefore, of considerable importance.

The area is bounded by arable land on the north-west and the south-west sides, by the extensive woods round Walcot Hall on the south-east side, and by meadows and parkland next to the village of Barnack on the north-east side. The area forms a rough rectangle with its longest sides pointing south-east. A good many arable species have found their way in along the edges nearest the fields, and also woodland species along the side of the wood. A number of oak, birch, hawthorn, etc., seedlings, which have spread in from the wood, have established themselves over the area, getting thinner the farther they are from the wood. This suggests that, if the burning is discontinued, scrub would soon grow upon the area and eventually it would revert to woodland. As to the surface of the ground, it is exceedingly irregular and consists of a succession of mounds and troughs. The depth between the top of a mound and the bottom of a trough varies greatly, but may be as much as 20 ft., producing a slope of nearly  $45^{\circ}$ , but this is exceptional, and in other parts of the area the undulations are not nearly so steep. Pl. 1, photos. 1 and 2 give some idea of the nature of the surface, and phot. 2 also shows the establishment of oak seedlings on the south side of the area. The prevalence of oak seedlings here rather than ash, which is the usual pioneer on the chalk, is probably solely due to the Walcot wood consisting largely of oaks, like all the local woodlands. Ash seedlings occur, but not in any number.

#### GEOLOGICAL FORMATION AND SOIL

The area lies entirely on Jurassic strata, the most important representatives of this series being the Inferior Oolite or Lincolnshire limestone, and the Upper Estuarine beds of the Great Oolite. The relation of these beds to each other and to the rest of the series is illustrated in the accompanying simplified section (Fig. 1).

The Lincolnshire limestone is composed of a series of oolitic limestones displaying different characters in various localities. Two main characteristics can be mentioned:

- (1) *Coralline facies*: Limestone abounding in corals mainly converted into finely crystallized calcium carbonate.

(2) *Shelly facies*: Limestone consisting almost wholly of small shells, fishes teeth, etc., either water-worn or encrusted with calcium carbonate.

At Barnack the shelly facies predominate.

The importance of the Upper Estuarine beds of the Great Oolite at Barnack lies in the fact that the junction of this series with the Inferior Oolite is marked by the ferruginous mass of the 'Ironstone junction band' which everywhere lies on top of the Lincolnshire limestone. Although the horizon of this band and the Lincolnshire limestone does not actually occur in the area of the

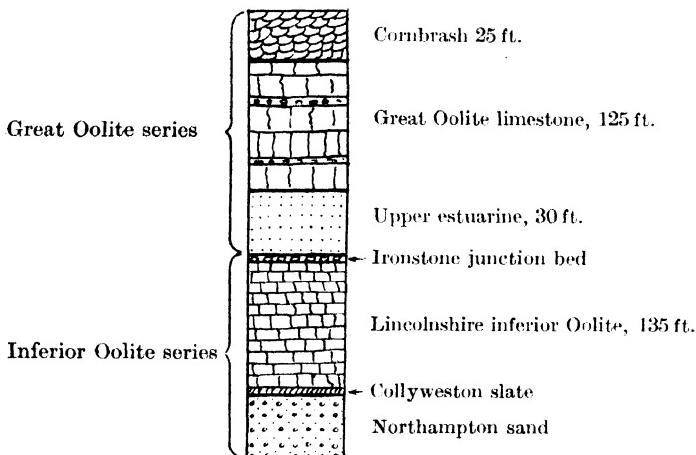


Fig. 1. Simplified section of Jurassic strata.

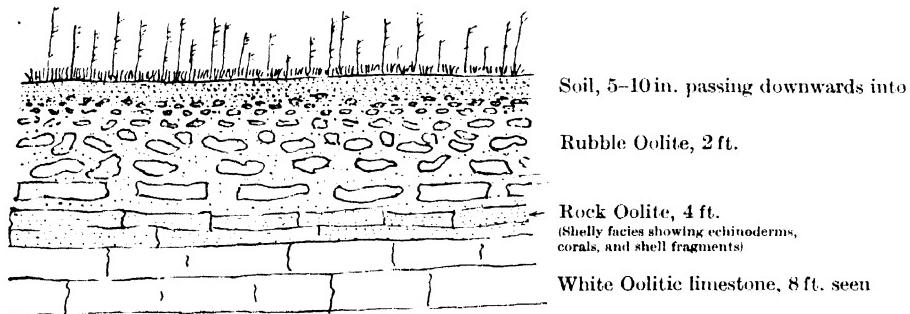


Fig. 2. Section of pit in Lincolnshire oolite at Barnack.

'Hills and Holes' (it lies about a mile to the east), its effect is seen in the upper portions of the limestone by a distinctly red ferruginous grit. The agricultural land formed on the Lincolnshire limestone is light and porous and generally markedly red.

The excavations of the 'Hills and Holes' continue into Walcot Park to the south, and here some of the pits afford a valuable illustration of the profiles typical of the area. Fig. 2 shows a typical exposure. It is obvious that in the area studied the vegetation must cover piles of debris and excavations

down to the rock, so that this profile will not always be closely followed. At the same time a top-soil varying in depth from 5 to 10 in., and in colour from dark grey to black, always containing considerable amounts of limestone in small pieces, seems typical over the whole area. This is followed either by rubble oolite in situ, or by debris from the quarrying which produces much the same effect. In all cases the humus layer gradually shades off into the subsoil of larger rock fragments. The profile would seem to be typical of the so-called 'rendzina' formed from limestone. It was noticed that the humus layer was generally thicker and darker in the troughs than on the sides of the mounds, but nowhere showed any signs of acidity. Pl. 1, photos. 3 and 4 show the top section of an exposure on the 'Hills and Holes' area itself.

A number of *pH* values were taken over the area, and it was found that the average value for the top inch of soil anywhere was 7.2. The *pH* of the main rooting area and of the subsoil remained very constant over the whole area at 7.4–7.5. The marked alkalinity of the soil in the troughs as well as on the 'hills' accounts for the fact that there is no great difference in the vegetation growing over the area.

In addition, rough mechanical analyses were carried out with specimens of soil taken from the main rooting area in various places. These yielded the following average results and confirm the very light and porous nature of the soil:

Stones and gravel (particles above 3 mm.)	49.0%
Fine gravel (particles 3–1 mm.)	15.5%
Coarse sand (particles 1–0.2 mm.)	17.0%
Fine sand (particles 0.2–0.04 mm.)	12.0%
Silt and clay (particles below 0.04 mm.)	6.5%

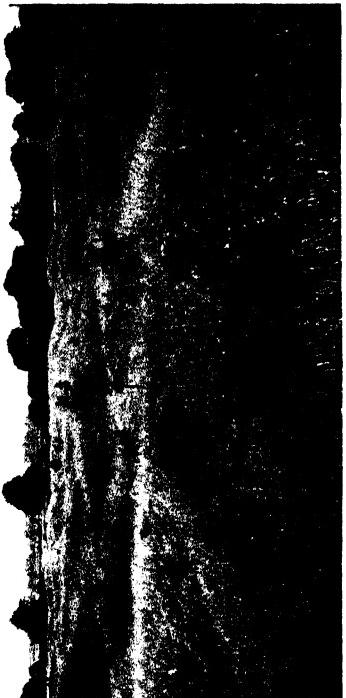
Determinations of the percentage of calcium carbonate in the same rooting area yielded an average result of 53.5.

#### VEGETATION

The two grasses, *Bromus erectus* and *Brachypodium pinnatum*, appear to be dominant over the area. As a rule *Bromus erectus* appears to be more dominant on the 'hills' and *Brachypodium pinnatum* in the 'holes', but they are closely intermingled. A close sward is rarely produced on the sides, and frequently not on the tops of the 'hills', with the result that the occurrence of the rarer flowering herbs here is greater than in the 'holes'. In late summer, and particularly after a drought, the vegetation in the 'holes' appears considerably greener than that on the 'hills'. This is due in part to the greater desiccation produced on the slopes where drainage is rapid and less humus is present, but also to the greater proportion of *Brachypodium*. Owing to the fact that the soil in the 'holes' is still definitely alkaline, there is no marked difference in the composition of the vegetation there compared with that on the 'hills' beyond the fact that the herbage is much closer and the thickly growing grasses have choked out a number of the more tender herbs. Even so,



Phot. 1. North end of 'Hills and Holes' showing Barnack village and church.



Phot. 2. South end of 'Hills and Holes' showing oak seedlings colonizing from Walcot wood.





such strong growers as *Poterium Sanguisorba*, *Helianthemum Chamaecistus*, *Lotus corniculatus*, *Galium verum*, etc., are nearly as plentiful as on the sides of the 'hills'. The not very continuous herbage on the 'hills' has an average height of 5 in. with the flowering stems of *Bromus erectus* rising through it to nearly 2 ft. On the flatter portions and in the 'holes', where the turf is very much more continuous, the height of the herbage averages 10-12 in., and is occasionally even taller.

With a view to gaining a reasonably accurate picture of the relative abundance of the commoner plants over the area, fifty separate 1 ft. squares were taken at random over the area and the different species occurring within them noted. If the number of squares in which any particular species occurs is multiplied by 2, a percentage frequency figure is obtained which gives the relative abundance of the species. This method furnishes a useful check on the purely subjective frequencies given in the complete list of species found within the area. The order of frequency of the commoner species comes out more or less as was expected. The ubiquity of *Poterium Sanguisorba* is very striking, but the extremely general occurrence of *Cirsium acaule* and *Pimpinella Saxifraga* had not been realized before the count was made.

The following are the results of the count in order of frequency of occurrence:

	%		%
<i>Bromus erectus</i>	90	<i>Astragalus danicus</i>	
<i>Poterium Sanguisorba</i>	88	<i>Lathyrus pratensis</i>	
<i>Brachypodium pinnatum</i>	76	<i>Leontodon hispidus</i>	
<i>Helianthemum Chamaecistus</i>	68	<i>Plantago lanceolata</i>	
<i>Hieracium Pilosella</i>	50	<i>Primula veris</i>	
<i>Lotus corniculatus</i>	42	<i>Rumex Acetosa</i>	
<i>Cirsium acaule</i>	40	<i>Aceras anthropophora</i>	
<i>Festuca ovina</i>	34	<i>Achillea Millefolium</i>	
<i>Galium verum</i>	24	<i>Alopecurus myosuroides</i>	
<i>Pimpinella Saxifraga</i>	24	<i>Anemone Pulsatilla</i>	
<i>Linum catharticum</i>	20	<i>Arabis hirsuta</i>	
<i>Avena pubescens</i>	16	<i>Campanula glomerata</i>	
<i>Asperula cynanchica</i>	14	<i>Carlina vulgaris</i>	
<i>Briza media</i>	12	<i>Centaurea nigra</i>	
<i>Anacamptis pyramidalis</i>	10	<i>Cerastium semidecandrum</i>	
<i>Thymus Serpyllum</i>	10	<i>Hippocrepis comosa</i>	
<i>Plantago media</i>	8	<i>Phleum pratense</i>	
<i>Anthoxanthum odoratum</i>	6	<i>Ranunculus acris</i>	
<i>Filipendula hexapetala</i>	6	<i>Tragopogon pratensis</i>	
<i>Koeleria cristata</i>		<i>Trifolium pratense</i>	

The general flora of the quarries is rich and attractive and furnishes a succession of interesting plants. The majority of these are typical calcipetes. Starting with the bright violet, *Anemone Pulsatilla*, in early May, *Aceras anthropophora* is to be found in surprisingly large numbers by the end of the month. In June, *Astragalus danicus*, *Hippocrepis comosa*, *Gymnadenia conopsea*, *Ophrys apifera*, *Filipendula hexapetala*, etc., are all to be found in reasonable

numbers, whilst in July the sward becomes bright with many spikes of *Anacamptis pyramidalis* mixed with the less frequent *Campanula glomerata*, with occasional white patches of the small *Asperula cynanchica*. The openness of the turf is well illustrated by the occurrence of such plants as *Cerastium semidecandrum*, *Erophila verna*, *Saxifraga tridactylites*, *Myosotis collina*, etc., which would not be expected in a close sward.

The following is a general list of the species noted in the area, excluding the purely marginal agrestal and woodland species, which are listed subsequently. Those species most frequently occurring on the sides of the area, but also sporadically over the whole area, are marked with an asterisk. The flora in general differs very little from that of the chalk grassland.

<i>Aceras anthropophora</i>	o.-l.f.	<i>Galium verum</i>	a.
<i>Achillea Millefolium</i>	o.	<i>Geranium pusillum</i>	r.
<i>Alopecurus pratensis</i>	r.	<i>Gentiana Amarella</i>	r.
<i>A. myosuroides</i>	o.	<i>Gymnadenia conopsea</i>	o. one large patch
<i>Anacamptis pyramidalis</i>	f.	<i>Helianthemum Chamaecistus</i>	a.
<i>Anemone Pulsatilla</i>	o.	<i>Heracleum Sphondylium*</i>	o.
<i>Anthoxanthum odoratum</i>	f.	<i>Hieracium Pilosella</i>	a.
<i>Anthriscus sylvestris*</i>	r.	<i>Hippocratea comosa</i>	f.
<i>Anthyllis Vulneraria</i>	r.	<i>Hypericum pulchrum</i>	r.
<i>Arabis hirsuta</i>	o.-l.f.	<i>Koeleria cristata</i>	f.
<i>Asperula cynanchica</i>	f.	<i>Lathyrus pratensis</i>	l.a..
<i>Astragalus danicus</i>	f.	<i>Leontodon hispidus</i>	f.
<i>A. glycyphyllos</i>	r.	<i>Lepidium campestre</i>	r.
<i>Avena pubescens</i>	l.a.	<i>Linum catharticum</i>	l.a..
<i>A. pratensis</i>	r.	<i>Lolium perenne*</i>	r.
<i>Betula alba</i> seedlings	o.	<i>Lotus corniculatus</i>	a.
<i>Brachypodium pinnatum</i>	v.a.	<i>Medicago lupulina</i>	f.
<i>Bromus erectus</i>	v.a.	<i>Melandrium album*</i>	o.
<i>Briza media</i>	f.	<i>Myosotis collina</i>	o.
<i>Campanula glomerata</i>	o.	<i>Ophrys apifera</i>	r.
<i>C. rotundifolia</i>	f.	<i>Orobanche elatior</i> on C. Scabiosa	r. one good patch
<i>Carduus nutans</i>	r.	<i>Origanum vulgare</i>	r.
<i>Carlina vulgaris</i>	f.	<i>Pastinaca sativa*</i>	o.
<i>Caucalis Anthriscus</i>	o.	<i>Phleum pratense</i>	r.
<i>Cerastium arvense</i>	r.	<i>Pimpinella Saxifraga</i>	a.
<i>C. semidecandrum</i>	o.	<i>Plantago media</i>	f.
<i>Centaurea nigra</i>	r.	<i>P. lanceolata</i>	o.
<i>C. Scabiosa</i>	o.	<i>Poa pratensis</i>	l.a. a few patches
<i>Chrysanthemum</i>	r.	<i>Polygala calcarea</i>	r.
<i>Leucanthemum</i>		<i>Poterium Sanguisorba</i>	v.a.
<i>Cirsium acaule</i>	a.	<i>Primula veris</i>	f.
<i>Crataegus monogyna</i>	o.	<i>Quercus Robur</i> seedlings	o.
<i>Crepis hieracioides</i>	o.	<i>Ranunculus acris</i>	r.
<i>Cynosurus cristatus</i>	r.	<i>Reseda lutea</i>	r.
<i>Dactylis glomerata*</i>	o.	<i>Rumex Acetosa</i>	f.
<i>Erophila verna</i>	o.	<i>R. obtusifolius*</i>	r.
<i>Euphrasia nemorosa</i>	r.	<i>Sambucus nigra</i> seedlings*	r.
<i>Festuca ovina</i>	l.a.	<i>Saxifraga tridactylites</i>	o.
<i>Filipendula hexapetala</i>	f.	<i>Scabiosa arvensis*</i>	r.
<i>Galium Mollugo</i>	f.		

Scabiosa Columbaria	o.	Trifolium pratensis	f.
Senecio Jacobaea	r.	T. procumbens	o.
Silene Cucubalus*	r.	Trisetum flavescens*	r.
Sonchus oleraceus*	r.	Verbascum nigrum	r.
Stellaria media	o.	Verbena officinalis	r.
S. Holostea	r.	Veronica Chamaedrys	f.
Taraxacum officinale	r.	Vicia angustifolia	o.
Thymus Serpyllum	f.	V. Cracca	o.
Tragopogon pratensis	o.	Viola hirta	o.

*Bryophytes*

The following mosses have also been found in the area and have been kindly identified by Mrs R. Upcott. The list is in all probability not very complete. By far the most abundant moss is *Brachythecium purum*, which is also the most common moss in chalk grassland. In the barer patches, large amounts of *Bryum caespiticium* occur:

Brachythecium purum	v.a.	Fissidens adiantoides	o.
Bryum caespiticium	l.a.	F. taxifolius	f.
B. erythrocarpum	o.	Pottia recta	r.
B. capillare	o.		

*Marginal agrestal species*

The following species have been found along the sides of the area, near arable fields. This list includes some of the species included in the general list for the area, but all these species occur much more thickly along the sides:

Agrimonia Eupatoria	Ononis arvensis
Agropyron repens	Papaver Rhoeas
Anthriscus sylvestris	Pastinaca sativa
Bryonia dioica	Rosa arvensis
Cirsium arvense	Rubus fruticosus (agg.)
C. lanceolatum	Rumex obtusifolius
Convolvulus arvensis	Scabiosa arvensis
Crepis capillaris	Silene cucubalus
Dactylis glomerata	Sisymbrium officinale
Heracleum Sphondylium	Sonchus arvensis
Linaria vulgaris	S. oleraceus
Lolium perenne	Trisetum flavescens
Melandrium album	

*Marginal woodland species*

The following species have been found along the edge of Walcot wood on the south side of the area:

Acer campestre	Nepeta hederacea
A. Pseudo-platanus seedlings	Poa nemoralis
Arctium Lappa	Prunus spinosa
Bellis perennis	Quercus Robur seedlings
Betula alba seedlings	Sambucus nigra seedlings
Fraxinus excelsior seedlings	Ulmus sativa seedlings
Ligustrum vulgare	Urtica dioica
Listera ovata	Valeriana officinalis
Mercurialis perennis	

*Helpstone quarries*

Some evidence that the 'Hills and Holes' vegetation is the typical grassland of the Inferior Oolite in this district is forthcoming from Helpstone quarries, which lie some 3 miles to the east of Barnack and portions of which are still being worked. Here exactly the same type of habitat occurs, a thin stony soil over old quarry workings, with an irregular surface of mounds and slopes. The strip of grassland here is, however, much narrower, with the result that many more cornfield weeds are to be found. Apart from this, the whole vegetation bears a remarkably close resemblance to that at Barnack. On the whole there seems to be more *Brachypodium pinnatum* here than *Bromus erectus*, but this has not prevented the vigorous growth of nearly all the Barnack specialities. There is the same profusion of *Poterium Sanguisorba*, *Helianthemum Chamaecistus*, *Hieracium Pilosella*, *Galium verum*, *Cirsium acaule* and *Lotus corniculatus*. The only relatively rare species occurring at Barnack which was not found at Helpstone was *Arabis hirsuta*, though a search rather late in the year only produced one plant of *Anemone Pulsatilla*. A feature different from Barnack is the much larger number of plants of *Origanum vulgare* and *Reseda lutea* which are found at Helpstone. In addition, *Calamintha Acinos*, which was not noted at Barnack, occurs here.

This area has not been studied systematically, but the following list gives an idea of the general flora which occurs. Obvious cornfield intrusions have not been included and frequencies have not been attempted:

<i>Aceras anthropophora</i>	<i>Gentiana Amarella</i>
<i>Achillea Millefolium</i>	<i>Gymnadenia conopsea</i>
<i>Anacamptis pyramidalis</i>	<i>Helianthemum Chamaecistus</i>
<i>Anemone Pulsatilla</i>	<i>Hieracium Pilosella</i>
<i>Anthyllis Vulneraria</i>	<i>Hippocratea comosa</i>
<i>Asperula cynanchica</i>	<i>Leontodon hispidus</i>
<i>Astragalus danicus</i>	<i>Linum catharticum</i>
<i>Brachypodium pinnatum</i>	<i>Lotus corniculatus</i>
<i>Bromus erectus</i>	<i>Medicago lupulina</i>
<i>Briza media</i>	<i>Ophrys apifera</i>
<i>Calamintha Acinos</i>	<i>Origanum vulgare</i>
<i>Campanula glomerata</i>	<i>Pastinaca sativa</i>
<i>C. rotundifolia</i>	<i>Pimpinella Saxifraga</i>
<i>Carduus nutans</i>	<i>Poterium Sanguisorba</i>
<i>Carlina vulgaris</i>	<i>Reseda lutea</i>
<i>Centaurea nigra</i>	<i>Scabiosa arvensis</i>
<i>C. Scabiosa</i>	<i>S. Columbaria</i>
<i>Cirsium acaule</i>	<i>Senecio Jacobaea</i>
<i>Euphrasia nemorosa</i>	<i>Thymus Serpyllum</i>
<i>Filipendula hexapetala</i>	<i>Tragopogon pratensis</i>
<i>Galium Mollugo</i>	<i>Vicia Cracca.</i>
<i>G. verum</i>	

In conclusion, the author would like to express his thanks to Prof. A. G. Tansley for his kind help and advice.

# BURTT MEMORIAL SUPPLEMENT

## SOME EAST AFRICAN VEGETATION COMMUNITIES

BY B. D. BURTT

EDITED BY C. H. N. JACKSON

WITH A FOREWORD BY W. H. POTTS

(*With Plates 2-27, containing Photographs 1-52*)

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## FOREWORD

My late colleague, B. D. Burtt, first came out to Africa in October 1925, and from then till his death in June 1938 found all his interest in the African world, particularly in the collection, observation and recording of its rich flora. Filled with intense enthusiasm for natural history and gifted with the keenest powers of observation, he gradually accumulated a unique knowledge of the plants of the savannahs of East and Central Africa so that at the end it was not only a delight, but also a challenge, for him to encounter in his own woods a tree or shrub to which he could not give a name. At first content mainly with the collection of plants and the acquisition of knowledge of their diverse forms, their distribution and their natural associations, he refused premature attempts to integrate this knowledge and to theorize as to the evolution of the various plant associations that he quickly came to recognize; but these and kindred problems were always at the back of his mind even in the early days, as the following extract from his diary shows, and he thought much about them, and directed his observations towards their solution.

‘Tuesday May 12th, 1926. Passed the first Zigi forest and plantations of Cassava, making notes of the glens that cut down into the savannah hills, i.e. *Sterculia* was seen sheltered by *Albizia brownii* and *Albizia* sp. [? *zygia* or *fastigiata*], a young tree with smooth trunk. Another young *Sterculia* occurs in the secondary thicket above the Zigi plantation, while many others were noticeable in the young forests and old savannahs. Leaving the road I climbed the savannah slope to the summit of the largest of the central hills; the grass stood four to six feet high all the way up, while savannah trees of the Zigi valley type stood isolated among the grass, many having charcoal adhering to the bark, and dead bits of *Platycerium angolense*, an epiphytic fern characteristic of the Zigi hill savannahs, adhering to their trunks and major branches. [Here follows list of trees noted.] The uniform size of these trees was noticeable, and the even distribution of species. The fire must have been very strong, as all climbers had been eradicated and the young shoots of *Smilax kunthianum* and *Vigna* were becoming evident.

‘Working along the summit of the hill I came to a dense thicket of the trees mentioned before that had escaped the fire. *Smilax* and *Paullinia* with *Vigna* had bound the trees together, making an impassable tangle; cutting a way through I came to an older savannah that had not been burnt for some years, and following this I made a descent of the hill towards the low forests of the plains. The tangle of *Toddalia* overhead produced heavy shade, while other great thorny lianes climbed the stems of the savannah trees. The presence of healthy *Platycerium* gave evidence of the lack of fire. Among the savannah trees I came across *Chrysophyllum* sp. (small narrow leaves), “Mvule” (*Chlorophora excelsa* Benth. & Hook. f.), and “Mkusa” [it has not been possible to

identify this name] growing above the savannah, and also the beginning of evergreen undergrowth. This slope is evidently reverting to forest.

'This young forest opened out into an area that had been fire-swept. It was composed of very old savannah trees, one, *Markhamia lanata*, being over 30 ft. high and having a bole 1½ ft. in diameter, the largest I have yet seen. Additional trees of *Strychnos* (20 ft. and very spreading), *Commiphora* (15 ft., gnarled), and an *Acacia* bush (12 ft., young) were noted, but the bush remained similar to that described early on. This bush continues down the lowest slope of the hill, where it is replaced by young forest with evergreen undergrowth and no grass.'

'The edge of the young forest was sharply defined from the savannah by the action of fire, no secondary growth having had time to spring up. [Here follows list of more trees seen.] Passing this forest I came to a narrow mbuga fringed with *Bridelia*, *Parkia* and *Flueggia*; *Carex* and grasses filled the flat ground. Passing this I came to the low forest level and, making a pathway, ascended to the summit of a little hill in the centre of it. This lowland forest is a mixture of the old savannah and young forest. The following savannah trees were noticed right into the forest: *Cussonia angolensis*, *Markhamia lanata*, *Stereospermum kunthianum*, *Bridelia*. These trees were being crowded out by *Afzelia*, and *Albizia fastigiata*, with the following forest trees: *Chrysophyllum msolo* (Engl.), *Chrysophyllum* sp. [? *C. natalense* or *C. zimmermanni*], "Mvule", "Mkusu", and *Boscia*.'

These extracts from the record of a day's wanderings show how, even though little more than half a year in this new country, Burtt was already not only recognizing different vegetation associations, but also noting the effects of grass fires on succession; this interest in the dynamics of plant ecology was maintained throughout his time in Africa, aided by the interest and knowledge of his Director, Mr Swynnerton, who shared his enthusiasm for these things. As his experience grew, he came to entertain more and more comprehensive views on the subject. It is the greatest tragedy of his premature death that he was just about to record these views and to formulate his conclusions. Unfortunately, practically nothing of this was committed to paper, and has so died with him.

In the paper which follows, Dr Jackson has collected together such accounts of the vegetation of East and Central Africa as are available in Burtt's departmental reports, and supplemented these by records from Burtt's diaries, field notes, and herbarium catalogues, and by his own considerable knowledge of the East African vegetation. He has thus, I think, succeeded in producing a valuable descriptive record of the vegetation of a large portion of this part of the world, and has presented a cohesive picture, much of which has hitherto been locked up in herbarium records and scattered botanical descriptions. By adhering to Burtt's own words this picture reproduces the vivid enthusiasm of his personality. I propose to supplement this by quoting verbatim from

Burtt's diaries a few more extracts not so directly concerned with the description of vegetation, but which will illustrate the manner of life he delighted to lead, and—more important—which will give the background against which he collected the information contained in this paper.

Here then is the record of one of Burtt's very early days; he had been three months in Africa:

'3. 1. 26. *Sunday.* Most gorgeous sunrise. The horizon was the colour of red magnesium light [probably strontium meant]; this colour faded into the palest blue (moonstone); it lasted only a few minutes. With a weird-looking crowd of local men I set out at 8.00 a.m. to climb the next mountain on the road to Kibaya, to survey the land. I am to make a clearing there.'

'Passed on to a number of shambas and to an mbuga beyond the hills. The grass was  $1\frac{1}{2}$  ft. high but thin, and beautiful to look at. The mbuga was full of butterflies. Hartebeests grazed in the centre, and a flock of ostriches, of which three were fine males with plumes; they ruffled them in front of the hens a good deal. Attempts to reach the hartebeests were of no avail, as they ran off every time. Five giraffe strode about looking even more absurd in the open than they do among the trees. Spoor of eland, old, was common. Lovely birds in the mbuga. Found some lovely great Emperor larvae on *Combretum*. Male (blue, black and white) and female (brown) *Hypolimnas*. Lion footmarks on the path (NEW!). Late back to camp and rather tired. C. arrived and we had a good chat about people we knew. 10 p.m.—bed.'

This day's record is typical of the range of Burtt's interests; delight in the beauties of nature lends relish to the early start on a day's survey of future work, which is further lightened by the sight of one of Africa's unique features, its teeming game animals. Then follow observations on the insect world, to him a never-failing source of interest. And so, finally, after that interval of social contact in which he always delighted, to bed.

Incidentally, a hill was always a challenge, and there was many a sigh of regret when time, or obdurately lazy companions, prevented the conquest of an interesting looking one; here is a note from a later diary, during his Nyasaland journeys: 'Peaky mountain before us—needs climbing!'

As the years pass, delight in the country and its creatures does not diminish, and the plants are recorded with increased assurance and certainty; here is his account of three days during 1935:

'Tuesday.—With S. to Isanja village clearing camp—view clearing from large rock about the camp—then proceed southwards passing a small thicket with *Acacia hermannii* to the great Manyigi mbuga—gameless, with Tamarisk marking the course of the river, and the Rift Wall cliff-like and imposing. On return, visit and bathe in the hot springs at Manyige village, a deep pool of water  $75^{\circ}$  C. Night—with old F. and S. sleep out at the water hole below the clearing and see fourteen rhino—at one time four together. Some cows and a

calf, and one male, drink at the pool. Besides rhino we saw impala and zebra at the pool and heard lion, elephant and buffalo.

‘Wednesday.—Explore the bush beyond the pool—thick fly to clearing edge, carry a young male and hungry old male back across the clearing to camp. Night with S. and F. to Malawa water, but only see bushbuck.

‘Thursday.—Five miles back along road explore bush to east. Thin fly near Kinyangudi village. Night at water hole; see three rhino—one very fine one—also impala and zebra, but get cleared out by siafu [driver ants].’

Then there is this account of another night and day about a week later—a different pool this time:

‘During the night the pool is again visited by a very nervous male rhino which runs away snorting—then by some eland licking salt—then by buffalo which I do not see—then by a male rhino with a large horn—then by yesterday’s female and baby rhino which are very fearless and drink a long time. Morning—breakfast at camp, then car reconnaissance up the scarp; fly all the way up to foot of hill 5½ miles from camp. Fine trees of *Monotes* and *Brachystegia microphylla* on high land with *Strychnos pungens* and *Randia sericantha*, some *Brachystegia* coming to leaf. Fly obviously living on “hog’s back” of miombo. Evening—to hot spring and bathe, very refreshing; then to tree (above pool), come on herd of cow buffalo and youngsters at 100 yards and wound one unfortunately. In a very short time five rhino come and drink. On way to *machan* see a fine cow eland and crested guinea fowl.’

This after having described the previous night (spent in same manner) as ‘very uncomfortable’.

The experience of later years enabled him to draw such records as this from fleeting glimpses from a railway train:

‘12. 4. 36. Morning—pass Malagarasi with interesting escarpment, *Isoberlinia-Brachystegia* country and peculiar gall acacia on slopes having a very upright habit, the same as seen at Uvinza. The train follows down the subsidiary rift of the Malagarasi system. Bush entirely miombo with stands of *Isoberlinia densiflora* with enormous leaf and small habit (20 ft.); *Isoberlinia globiflora* and *Acacia holstii* in flower. About halfway to Kigoma we pass through peculiar semi-evergreen forest, very dense, looking like *Cynometra* and a species of *Pterocarpus* some of which is in flower.’

And here another from the same year, shows how he takes advantage of the early docking of the steamer, on a voyage down Lake Tanganyika, to increase his knowledge of the countryside:

‘Arrive off Kelema at about 2.30 [p.m.]. Undulating country rather like the Simbo hills. Landing at 3.30, walk up the main street, a quarter of a mile long, with avenue of fig trees (bark cloth). Very polite natives. Walk along coast, innumerable dug-out canoes; then climb up rocky slope with 6–7 ft. grass; *Hyparrhenia*, *Trichopteryx* and a rather nice *Andropogon* (not collected). Shrubs all coppiced *Diplorrhynchus*, *Terminalia*, *Combretum*; *Brachystegia*

(with stipules and olive green leaves) [*B. allenii*]; *Isoberlinia*; *Sterculia* nr. *quinqueloba*; *Acacia holstii* (flowering); *Acacia* sp. unknown; *Commiphora pilosa* (very common); *Bauhinia petersii*; *Entada* with broad leaves; *Triaspis*; among the grass on more open ground is a very attractive lavender flowered *Tinnea*. Grass very tall and disagreeable walking. After about 2 miles descend by a steep path to a sandy bay with much crocodile spoor. Take 3 female and 7 male *Glossina palpalis* in the bay, 3 empty puparia under thicket in sand—it surprised me to see *palpalis* in this bay, as there was no real forest, only *Isoberlinia-Brachystegia* hills to the coast and the bushes on cliffs! Ambatch flowering on the beach.'

Here is Burtt's idea of a day of rest—a Sunday on safari in the Abercorn district (1936):

'Up at dawn, and by canoe up river and see more hippo. Kalambo fall audible from canoe. Lovely king-fishers. Catalogue plants. Morning walk along coast to south and collect Aloes; a small *Aristolochia* with black flowers, *Commiphora pteleifolia* and the *Euphorbia* and a white Acanth.—extremely hot. Afternoon—catalogue plants. Write up *palpalis* situation. Large crocodile swimming about out of range; view of lake very fine; bathe and watch *G. palpalis* hunting along the shore. Hippo come out and make a lot of noise at dark.'

Later on in this *safari* he notes in the diary: 'The Kituta bay is interesting in its series of crescent-shaped old lake beaches.' There was no more than this sentence—but the observation formed the basis of subsequent investigation into the history of the lake tsetse in that area and a very interesting section of his final report dealing with the influence of changing lake level on the fly.

A Saturday excursion in the Abercorn area (1936):

'Miss G. and I set off and leave the car at the new fly picket; follow old road then hit off towards the scarp—in very tall grass with much blue *Blepharis*—come to huge open swamp with fresh buffalo spoor—rise up through dense old cultivation to stony *Isoberlinia-Brachystegia* hills with poor grass and much *Leptactinia* and the straggly *Combretum* with green fruits; climb up to cliff with *Burttia*, *Vellozia* and Aloes of the lake variety—then on to the top of the scarp at a survey beacon—and colossal view of the lake, and all the Abercorn area. Near top collect a small spiny *Euphorbia*, and a climbing *Combretum*; after lunch descend a ravine, and come out above a great chasm of a dry waterfall, covered with hanging Aloes, *Burttia* etc. etc.—a wonderful place. Climb back to ridge and descend to car. New picket caught fly on boys coming from Abercorn.'

And thus was business combined with pleasure, and a new fly picket kept up to the mark.

One side of the knowledge gained in the course of such wanderings as have been described above was luckily left in such a state that it could be published for the benefit of his successors. This was a key designed to enable the tyro

without botanical knowledge to identify the plants of the upland savannahs of East and Central Africa, using purely vegetative characters such as leaf form and arrangement, bark, and the general habit of the trees. One part of this, put into shape by his colleagues, has already appeared, printed by the government of Tanganyika Territory; the war has prevented publication of the second part which needed more preparation, but it is now all ready as soon as conditions permit its appearance.

The other side of Burtt's knowledge, the description of the vegetation as a whole and the distinguishing of its natural associations and groupings, remained unrecorded save in the shape of scattered reports and notes, lacking cohesion. It is the object of the following pages to gather together the material left and present as coherent a picture as possible under the circumstances. But it will be readily understood that the result, as Dr Jackson himself points out, of necessity misses the completeness which Burtt himself could have given to it; the account suffers inevitably from an unevenness of treatment which he himself would have been able to remedy from his own unrecorded fund of experience and knowledge. And, finally, it lacks the integrative treatment which Burtt's thirteen years of experience and close observation was just beginning to enable him to supply. As it is, it forms the best record that remains of his contribution to the knowledge of East African plants, and it is for this reason that the Committee administering the funds subscribed for a memorial to Burtt and Swynnerton have considered a contribution towards its publication the best possible use for a large portion of the sum available.

#### I. INTRODUCTION

Though Burtt collected plants in almost every District of Tanganyika Territory except the south-east, and though data for all these specimens exist, I have had to confine my selections for the present survey to those regions upon which he has reported fairly fully himself, or with which I happen also to be familiar. The data selected in this way are sufficient to enable me to compare the vegetational changes on two lines, roughly southwards from Lake Victoria as far as Lake Nyasa on the one hand, and south-eastwards to the mountains of Morogoro, overlooking the African coastal plain, on the other.

All Burtt's actual descriptions are in inverted commas. They are from Departmental reports, mostly accounts of tsetse-fly surveys, and it should therefore be understood that he did not originally intend them as contributions to a general account of the vegetation of this region. It has been necessary to take liberties with their sequence in order to combine them for the present purpose. At the same time, Burtt's vivid and individual style seems to justify as close an adherence as possible to his original writings.

So far as possible I have given Burtt's own descriptions of each link in the two chains of vegetation, but in the table which follows the descriptions I have

had to omit or amalgamate some of them, because naturally Burtt's lists and descriptions refer sometimes to a Province, sometimes to a District, or again perhaps to some quite local conditions such as those in the Lukosi valley of the Usagara mountains, or the trough of Lake Rukwa.

This arrangement inevitably results in some overlapping and in some unevenness of treatment. For example, the miombo is the most widespread community, and its changes in composition can be followed fairly completely along each of our two transects. On the other hand, the thornbush communities in the region dealt with are most varied and widespread in the Central and Lake Provinces of Tanganyika Territory, to which therefore nearly all the descriptions of them refer, and there are only a few notes on the occurrence of isolated thornbush types to the south. Also, of course, much of the thorn country merges into thicket; and many of the thickets are riverine or confined to termite mounds.

In several of his descriptions of foliage, Burtt has used the expression 'olive green'. This should always be taken to mean the blue- or grey-green of the olive grove, and not the true olive green of its fruits.

The descriptions of vegetation in Tabora District have been written by me, and should be taken to refer only to those parts south of the railway, north of which the country has more affinity with Kahama on the one hand and the Central Province on the other.

In order to emphasize the sequence of changes along the two lines chosen, I have arranged Burtt's account so as to follow through a single vegetation type at a time, and the types I have separated in this way are:

- (i) Miombo woodland (*Isoberlinia-Brachystegia* savannah).
- (ii) Thorn savannah (deciduous *Acacia* and *Commiphora* types).
- (iii) Deciduous thicket.
- (iv) Combretum communities.
- (v) Highland grassland.
- (vi) Evergreen forest and riverine communities.
- (vii) Termite mound communities.

Authors' names are omitted in the text, but those belonging to the woody plants will be found in the Table in § IX.

## II. THE MIOMBO WOODLAND (*ISOBERLINIA-BRACHYSTEGIA* SAVANNAH)

### 1. GENERAL (PHOT. 1)

'A very large proportion of the higher country is clothed with miombo—from which the native obtains bark for his grain bins, "kamba" or bark rope for building purposes; and it forms a favourite field for the honey hunter. A month before the rain sets in, the miombo-covered hills burst all at once into flaming reds, salmon pinks and coppery tinges of all hues, as the *Brachystegia*

trees flush into young leaf, and within a week all this riot of colour has blended into a forest of the freshest green, carpeted with a legion of flowers, some (*Kaempferia aethiopica*) recalling blue crocuses; and, in the Manyoni-Kazikazi miombo of the western Central Province, the white cushions of waxy star-like flowers (*Leptactinia benguellensis*) resembling a "super-jasmine" and scenting the air with fragrance rivalling narcissus.

'In full leaf the miombo forest is delightfully cool and shady, and the scanty grass (a feature of this woodland especially in the Rift Valley, Manyoni and Kazikazi areas) is pleasant to walk through. The miombo woodland greatly resembles the oak woods of the New Forest in England, only the trees are perhaps not so high, 30 to 40 ft., and more or less flat topped. But the bark looks almost the same. Closer observation will show that all the leaves are pinnate—while, in November, the activity of honey bees among the spikes of green flower heads in the tree tops of *Brachystegia spicaeformis* is quite phenomenal. Later in the season, when this tree is laden with flat green pods, *Isoberlinia globiflora* comes into flower. It often comprises half the woodland, and its bunches of flowers are borne well above the leafy canopy in loose racemes, which later develop into brown velvety pods.

'In the dry season, what a change! The whole miombo forest becomes entirely leafless, while grass fires burn up all the grass and leaf litter (Phot. 9, 10). The sun beats down unmercifully and whichever way one turns one sees the same view, the grey stems of the miombo trees fading into the shimmering distance. The buzz of insect life has vanished except for the sharp hiss of tsetse; brown dry pods up in the tree tops split suddenly and scatter their seeds; while, overhead, the bark of Batteleur's eagle will momentarily catch the attention, or, flitting before one from tree to tree, will move a flock of helmet shrikes, dismal white, black and grey birds emitting their mournful call as if they too are tired of the heat.

'When passing through the monotonous vastness of great forests of the miombo of the plateau, the eyes of the traveller are gladdened by the sight of a hill rising unexpectedly before him, clothed with an almost pure stand of flat topped, cedar like trees (*Brachystegia microphylla*) with feathery foliage, their dark smooth trunks with flaking bark (Phot. 2) contrasting sharply with the reticulate and silvery *Brachystegia* he has been passing through for hours. Small ferns *Pellaea hastata* and *Actinopteris radiata* grow from crevices between the rocks. The even grass of the miombo country gives place on the hill to a variety of attractive flowering plants such as *Haemanthus multiflorus*, aloes, *Bidens*, *Pycnostachys* and *Vernonias*, growing between the boulders in peaty soil. Large trees of *Sterculia quinqueloba* with their pale yellowish bark and expansive five pointed leaves are frequently seen on the hills, together with that peculiar tree *Albizia tanganyicensis* with cream-white trunk, peeling off papery shavings of old bark. The hills are a favourite resting place of eland, while klipspringer are usually found on them, especially on the more rocky parts.

'Where the hills are largely composed of granite boulders the soil is a sandy loam mixed with humus and may be of a grey colour, lying in cracks between the rocks. In some places the soil is of a reddish colour while in others it may be heavily charged with quartz-pebble debris.'

## 2. MWANZA

In this area, 'the *Brachystegia microphylla* woodland occupies all rocky outcrops. At Katungulu these magnificent trees occur within 300 yards of the coast of Lukinga Bay. The trees are of gigantic size, some being more than twelve feet in circumference at breast height, a fact which together with the gigantic proportions assumed by such trees as *Afrormosia* and *Isoberlinia* suggests the virgin qualities of the soil.'

'*Isoberlinia globiflora* forest dominates in the Karumo area. Many of the trees are of great age and size, trees of eight feet circumference occurring at hundred yard intervals and interspersed with much regeneration. In eastern Karumo *Brachystegia spicaeformis* is very rare but becomes commoner towards Mazinda, where unusually large trees are met with. Strangely enough *Pterocarpus angolensis* is almost absent, only a few small specimens being seen near Mazinda. *Ostryoderris stuhlmannii*, *Terminalia sericea* and *Commiphora fischeri* are rare, and where they occur are very stunted. *Burkea africana* occurs in central Karumo but is of no size; *Albizzia versicolor* on the other hand occurs as scattered trees of large proportions. The general impression of the *Isoberlinia globiflora* forest was that it had no signs of interference by natives for many hundreds of years.'

Relict trees of *Brachystegia microphylla* extend as far east as the town of Mwanza on Lake Victoria, and *B. spicaeformis* is found locally in the hills of Shinyanga to the south.

## 3. KAHAMA

'Travelling by train from Tabora towards Kigoma or northwards towards Mwanza, or, again, by road through Kahama to Biharamulo, the traveller passes through countless miles of miombo forest. He will if he is a keen observer notice that many of the miombo trees have feathery leaves and are different in appearance from those seen in the Central Province; these trees are *Brachystegia boehmii*. A feature of this vast miombo area is the wealth of other tree species associated with it, some of the more important ones being *Burkea africana*, *Swartzia madagascariensis*, *Afrormosia angolensis* (the last two plants are the native's favourite charcoal woods), *Pterocarpus angolensis* (the "mninga" furniture wood of up-country), *Monotes engleri*, *Diplorrhynchus mossambicensis* and many others.'

'This forest is well grassed for miombo, with stands of *Hyparrhenia rufa* and *Panicum maximum* three to four feet in height; it is also decorated with the handsome wine-red, Zinnia-like flowers of *Erythrocephalum* in the spring, and has certain characteristic aloes. As may be expected, this forest is well

burnt by grass fires, which keep down the abundant underbrush of saplings and suckers. The effect of fire exclusion is not yet established; field observation, however, suggests that considerable thickening would follow.

'Lichtenstein's hartebeest, and in the south sable and oribi, are the characteristic animals of this forest, and there are always a certain number of wart-hog and bushpig.'

'The soils may be of a rich terra-cotta red colour overlying a murram pavement, or near the hills may be deep and buff coloured, sandy in texture. In the lower areas where *Brachystegia boehmii* is common the soils are grey and of a clayey texture with grey fleckings about six inches below the surface.'

#### 4. TABORA

On rocky hills, the smooth trunks of *Brachystegia microphylla* (Phot. 2) or *B. bussei* (Phot. 3), the latter peeling to expose an orange-yellow layer, are everywhere encountered. North of Tabora, and again far south, *B. utilis* with rougher bark is met with on such outcrops; and on the elevated ridges about Kipembawe near the Mbeya border the late dry season is made gorgeous by the orange and red young leaves of *B. longifolia*, here with small and hairy leaflets resembling those of *B. boehmii*.

But over the great flat lands of the plateau, about 4000 ft. or under, *Isoberlinia globiflora* dominates in the miombo, and the widespread *Brachystegia spicaeformis*, with similarly rounded leaflets, is very common. Species with leaflets more elongate and feather-like are the delicate *B. wangermeana*, often adventuring forth into the edges of small seasonal swamps; *B. longifolia*, here with quite smooth leaflets characteristically glaucous below, and often forming almost pure stands bordering the flood plains of great rivers; and, dominating darker soils with a rich grass growth of *Trichopteryx*, the flat-topped *Brachystegia boehmii*.

Within the *Isoberlinia globiflora* woods, large trees of *Burkea africana* and its relative *Erythrophloeum africanum*, *Albizia antunesiana*, *Swartzia madagascariensis* with long, thin, sausage-like fruits, and *Pterocarpus chrysothrix* are specially characteristic of this area; and the usually smaller *Pseudolachnostylis maprouneaeifolia* and digitate *Paivaeusa dactylophylla* are more frequent than in other regions. *Pterocarpus angolensis*, more widespread, is also very common, its black crocodile bark conspicuous among the general silver grey.

The genus *Strychnos* is especially well represented. Besides the tall *S. heterodoxa* of the termite mounds, *S. innocua* and *S. pungens*, with its spined leaf tip, are abundant; and only less common are the two species with hooked and opposite spines, *S. spinosa* and the corky barked *S. schumanniana*. Other small trees deserving mention as being specially common in this area are *Diplorrhynchus mossambicensis* with milky latex and weeping habit, *Dalbergia nitidula* and *D. stuhlmannii*, *Hymenocardia mollis*, *Randia kuhniana*, *Holarhena febrifuga*, *Cassipourea mollis*, and *Psorospermum campestre* of which the

leaves are dull brown below. As usual, there are many Combretums; but *C. binderanum*, with scaly leaves and deep brown fruits, tends to replace the *C. zeyheri* so preponderant in the Central Province; the tall *C. grandifolium* is frequent along the margins of open glades, but its relative *C. gueinzii* is comparatively rare. Away from the termite mounds, *Commiphora fischeri* is the sole representative of its genus, and *Phyllanthus discoideus* the only important shrub, though here and there an evergreen tangle of *Landolphia petersiana* relieves the bare dry season monotony.

In this region, the miombo may often stretch uninterrupted over low crowns of the vast plateau, so flat that not a watercourse, not a single other vegetation type, intrudes for several miles. Farther west, on the borders of Kigoma District, the country is more dissected; here *Brachystegia longifolia* and *Isoberlinia densiflora* become very common, and there may be thickets of bamboo.

The dominant grass is *Andropogon* cf. *shirensis*, with some species of *Panicum*, *Eragrostis boehmii* (?) and occasional stands of the annual *Setaria rubiginosa*. The grass cover is mostly burnt about July, the fires hastening leaf fall which is maximal in August.

A feature of the Tabora area is the common occurrence on dark soil on the flats of extensive stands of *Brachystegia boehmii*, often giving place to *B. longifolia* near the contact with the flood plain of the Ugala river. Either species may form almost pure stands of large trees, but beneath is much regeneration of *Dalbergia*, *Combretum*, *Crossopteryx* and other genera, annually suppressed by the grass fires.

The dominant grass is *Trichopteryx superba*; but several species of *Andropogon*, notably *A. amplexens*, are present, and there is often a very dense growth of the annual *Hyparrhenia anthistrioides*.

Characteristic animals are the sable antelope, Lichtenstein's hartebeest, the southern reedbuck and Sharpe's steinbuck.

##### 5. MBEYA

'Miombo clothes the country north of Usangu whence it extends in a vast unbroken forest towards Tabora. It covers the low hills between Madibira, Ikoga and southwards towards Malangali, then follows along the escarpment which merges into the Elton Plateau and the Mporoto mountains forming the south-eastern margin of Usangu. The miombo woodland between the Ruaha and the Mporotos is composed of large well grown trees [mainly *Isoberlinia globiflora*] supporting good grass growth which is burnt annually; between Mapogolo and Ikoga it is found [*Isoberlinia globiflora* and *Brachystegia spicaeformis*] on a sandy type of soil supporting scanty herbage and simulating the miombo of Kazikazi on the Central Railway.'

Flying over Madibira to Mbeya, Burtt records:

'To the south-west the vast sea of *Brachystegia* extends towards Mbeya,

and the wall of the escarpment becomes a feature of the divide between the *Brachystegia* of the plateau and the gall-acacia swamp of the Usangu plains, separated from the *Brachystegia* by a band of *Acacia* spp. of variable width and composition. Nearing the south end of Usangu we fly over the Mporoto mountains which fill the gateway to Mbeya. A continuous strip of *Brachystegia* of the dry *burtii* type can be seen swinging across from the [western] Rift escarpment and connecting up with the [eastern] miombo strip which flanks the Livingstone mountains or Elton Plateau, rising steeply in magnificent topography from the great basin of Usangu.'

West of the Mbeya mountains, 'both sides of the [Rukwa] Rift valley are clothed with *Brachystegia* woodland falling in broken and steep scarps to the valley floor. It is of a poorly grassed type with trees of no stature. The soil lies in the form of flat terraces, or, more usually, is excessively stony. In all respects the country looks, in the dry season, like the more inhospitable parts of the Simbo hills in the Kondoa District, but the species of trees are different, being *Brachystegias* of the *boehmii* group with *Brachystegia burtii*, and *B. microphylla* on the tops of the hills. *Brachystegia* almost fills the south end of the Rukwa Rift valley between Lunga and Marenga, except where the woodland is broken by the narrow gorges of the Songwe and Sira rivers. This "plug" of *Brachystegia* occupies some of the most inhospitable country which I have ever seen; indeed so stony and scarred by gullies is this area that the *Brachystegia* trees themselves have the stunted appearance of coppice, while the place is subject to excessive heat at mid-day. Towards Njerenje the trees are larger and the road winds up for more than a thousand feet to this place, where a few cattle are to be seen. East and south-east towers the Mbeya range which is a natural mountain pasture.'

The higher hills of the Mbeya range are clothed with *Brachystegia floribunda* (Phot. 5), a species mentioned below in the Abercorn section of Northern Rhodesia.

#### 6. ISOKA, NORTHERN RHODESIA

'From Mwenzo [close to the meeting point of Tanganyika, Nyasaland and Northern Rhodesia] to Isoka and from Isoka to within six miles of Mbesuma the country is entirely dominated by *Brachystegia* trees of several species and resembles the hinterland of Abercorn and the Kasama and Mporokoso Districts. However, between Mwenzo and Ntekulu, on the Mwenzo-Abercorn road, *Brachystegia burtii* is dominant over large areas of highland country. This tree with its claret red flush (young leaf) and olive green foliage (mature) is found to extend southwards from Mwenzo for about twenty miles. At Isoka and behind Chunga farm and at mile 20 to 30 on the way from Isoka to Mbesuma are rocky hills clothed with *Brachystegia microphylla*. Between Isoka and Mbesuma near the Lungu stream is a fine forest of *Brachystegia spicaeformis*. The *Brachystegia* country as a whole is poorly grassed and at the time of my visit had not been burnt; the grass cover was scanty and nowhere more

than two feet in height. The *Brachystegia* woodland appeared to offer no possibilities for natural thickening by fire exclusion.

The *Brachystegia* woodland is intersected by waterlogged marshes locally termed "dambos" (Phot. 7). In many places these were still too wet to burn and carried a good stand of grass 3½ ft. in height. I am told that these dambos and most of the *Brachystegia* woodland are fired before the break of the rains.

'Large leaved *Isoberlinia tomentosa* (?) are a feature of the dambo margin and occur on large termite islands in them. A dambo often gives the impression of a wide road through the general monotony of the *Brachystegia* forest.

'*Uapaca* spp. (Phot. 14) and *Protea* spp. (Phot. 15) are widely spread, being commonest on the watershed between Northern Rhodesia and Tanganyika Territory. Within six miles of Mbesuma the road enters heavily thicketed rocky hills with valleys dominated by *Enterolobium africanum* while to the east for about one mile is a fine stand of *Afroformosia angolensis*'.

#### 7. ABERCORN, NORTHERN RHODESIA

'*Brachystegia* woodland dominates over most of the Abercorn District, the other vegetation types forming a very small part of the total vegetation.

'The *Brachystegia* woodland is divisible into various zones apparently limited by altitude. Whereas the *Brachystegia* of the high plateau and the *Isoberlinia paniculata-Brachystegia* woodland retain their leaves until just before the flush of young leaf takes place, causing an almost unbroken cycle of leaf cover, the *Brachystegia allenii* and *Isoberlinia globiflora-Brachystegia* woodlands have a long spell of leaflessness commencing in July and ending in December. When I revisited Abercorn in October 1936 the *Brachystegias* were in full young leaf and flower between 4500 and 6000 ft., while the whole Lake coast area between 2600 and 3500 ft. was bare and leafless. In all probability the Tanganyika Lake coast receives 25 to 30 inches of rain annually, while Abercorn itself receives 50 to 55 inches.'

'The low altitude Lake coast *Brachystegia* woodland clothes all the rocky hills fringing Lake Tanganyika in the Abercorn District; it is dominated by *Brachystegia allenii* (Phot. 4), a small tree with olive green foliage and rounded crown. *Monotes delevoyi*, *Lannea* and *Cryptosepalum* are seen in this woodland together with *Diplorrhynchus mossambicensis* and a small *Pterocarpus* (*P. chrysotricha*) with delightfully scented yellow flowers about May. The grass growth is comparatively poor, as the hillsides are largely composed of boulders.'

'The *Isoberlinia globiflora-Brachystegia* woodland, 3500 to 4000 ft., resembles very much the common and familiar woodland of the Central Province of Tanganyika Territory, but in the Abercorn District this type of woodland is rare being confined to the margins of the Isoko and Mswilo valleys, and the Mkoma dambo area on the road to Kalambo Falls. In all probability this woodland occurs as a fringe along much of the 3500-4000 ft. contour. It is

dominated by well grown trees of *Isoberlinia globiflora*, with *Brachystegia spicaeiformis*, *Combretum binderanum* and *C. sp.* (cf. *zeyheri*), *Diospyros mespiliformis*, *Terminalia sericea*, and near the Isoko dambo *Afrormosia angolensis*. Scattered trees of *Pterocarpus angolensis* and bushes of *Strophanthus eminii* are also frequent. The grass is mostly a thin stand of *Trichopteryx* with much exposed poor sandy soil.

'*Brachystegia bussei* (Phot. 3) is a very local type of woodland composed of tall smooth barked trees. They are to be seen in the woodland at the top of the Kalambo Falls; half way from Mpulungu to the Lunzua bridge on the Abercorn road; in the hills on the way to Mbete from Mpulungu; and near the Izi Falls. The soil in this woodland is usually of a bright red colour carrying poor grass growth.

'The *Isoberlinia paniculata-Brachystegia* woodland, 4500 to 5000 ft., dominates the country along the foot of the Chisungu escarpment. It is rich in tree species, containing much *Uapaca kirkiana* ("sand apple"), *Isoberlinia densiflora*, *Combretum psidiooides* and *Afzelia quanzensis*. The grass growth is medium and contains many coppice shoots of trees. The soil is reddish coloured and of typically acid nature; there is every indication that this vegetation community would densify with the exclusion of grass fires.

'The plateau *Brachystegia* woodland covers a vast area of Northern Rhodesia, and is characterised by *Brachystegia floribunda* (Phot. 5) which co-dominates with a small form of *Brachystegia longifolia*. *Monotes elegans* is exceedingly common, and also *Uapaca* and *Protea* of several species, one of which has very large pink flowers; *Parinari curatellifolia* is also common. The grass canopy is very variable, being usually 2 to 3 ft. high, but in some areas, bordering dambos, becomes much taller. The soil is of poor quality; the scattered native population follows the "chitemene" form of agriculture—lopping branches of trees, dragging them into a small area and burning them at the end of the dry season on the site of the future garden.

'Another type of *Brachystegia* clothes rocky hills from 5000 to 6000 ft. The rocky escarpment bounding the north side of the Saisi valley and Sunzu hill, Senga hill and Nakatali, Dundunda and Mbete hills are clothed with cedar-like *Brachystegia microphylla* (Phot. 7). Among the rocks occur the carmine flowered shrub *Dissotis melleri* and a remarkable candelabra *Euphorbia* (cf. *strangulata*). The rocks themselves are invariably covered with the fibrous plant *Vellozia splendens*, a cross section of the stem of which provides an admirable scrubbing-brush, while the natives use smaller branches of it for toothbrushes' (Phot. 6).

Though the dumbo marshes are not strictly *Brachystegia* woodlands, I insert here Burtt's notes on them, as the interesting stunted *B. taxifolia*, with dark yew-like leaves, is mentioned.

'The typical Abercorn dumbo (Phot. 7) is quite unfamiliar to the resident in northern Tanganyika Territory. It is usually a permanent spongy bog,



Phot. 1. The sea of the miombo in the dry season. Looking across a 'hog's back' at the base of the Rift Wall in Singida towards the Sandawe hills. *Isoberlinia globiflora* and *Brachystegia spiciformis* co-dominant (p. 73).



Phot. 2. *Brachystegia microphylla* on the Singida Rift Wall. Note the flaking bark and delicate feathery leaves (pp. 74, 76).





Phot. 3. *Brachystegia bussei* near Abercorn. Note the smooth bark flaking to expose the yellow layer below (pp. 76, 80).



Phot. 4. *Brachystegia allenii* near the Lake Tanganyika coast below Abercorn.  
The crown is rounded and the foliage bluish green (p. 79).





Phot. 7. *Brachystegia microphylla* near Abercorn. In the foreground is a typical dambro, with its centre of open grassland and fringe of small trees (pp. 79, 80).



Phot. 8. *Isoberlinia paniculata*-*Brachystegia* woodland in Nyasaland (p. 81).





Phot. 9. Woodland of *Isoberlinia globiflora* below the Singida Rift Wall. The scanty grass growth has been burned by the annual fire (p. 74).



Phot. 10. *Commiphora fischeri* in miombo woodland on the Singida Rift Wall; this shows well, as does also the above, the leafless dry-season aspect of the Central Province miombo, which lasts from May or June to December. On the southern transect the leafless period becomes progressively less, until in Abercorn it hardly exists (p. 74).



either resulting from almost permanent springs on the high plateau country which are the sources of the innumerable small tributary streams of the main rivers which are themselves permanent, or forming a fringe along the river valley fed by a parallel system of springs from the general flanking *Brachystegia* woodland. The presence of sundews (*Drosera madagascariensis*) suggests acidity of the soil. The dambos are very different from the black cotton soil "mbuga" type of country, which is lime-accumulating, is found in the thorn-bush areas of Tanganyika Territory, is only seasonally wet, and supports gall-acacias. The dambo may be a broad treeless shallow valley winding into the distance, or a long and narrow twisting glade, or the fringe of a swamp, in which case it is studded on its drier surface with shrubs of *Protea uhehensis*, *Hymenocardia mollis*, and, on the high plateau, is fringed by an abrupt wall of *Brachystegia taxifolia* (Phot. 6), as at Lake Chila. Some dambos, especially in the upper system of the Lufu tributaries, are studded with *Terminalia* trees with large silvery foliage, and another species with a form resembling *Uapaca kirkiana*. Trees of *Paivaeusa dactylophylla* are occasionally seen. The dambo moor contains a wealth of flowers, including *Kniphofia*, *Gnidia*, the beautiful blue *Coleus leucophyllus*, "yellow Iris" (*Moraea* sp.), *Dissotis* and many ground orchids.'

#### 8. BUA RIVER, NYASALAND

'The country rises gradually to approximately 4500 ft. towards Fort Manning, and the areas between the rivers rise imperceptibly into long low ridges which are traversed by many narrow grassy dambos some of which were still marshy at the time of my visit. The rivers and dambos give the impression of wide lanes through a monotonous uniform sea of woodland. The altitude of the plateau is more than 4000 ft., and is sufficiently high to enable ground frosts to take place in the valleys in late July and the beginning of August.

'The vegetation of the area is largely short grassed miombo woodland of uniform composition, and is of extreme monotony. The miombo woodland comprises about two thirds of the whole area. It extends far north to Kasungu and the Fort Alston game reserve; and it extends southwards into Portuguese territory, being, in fact, part of the eastern edge of the great Northern Rhodesia miombo forest belt. Having just completed a survey of the Abercorn District of Northern Rhodesia and having also visited the Districts of Kasama, Mporokoso and Isoka, I was impressed by the similarity of appearance to the Bua miombo of the Northern Rhodesia miombo and the sameness of the species which compose it. The woodland contains poor grass growth and is dominated by *Isoberlinia paniculata* (Phot. 8) with trees of *Brachystegia longifolia* (?), *Brachystegia floribunda*, *Brachystegia utilis* and *Brachystegia burttii*; these occurred fairly generally in the composition of the woodland. *Brachystegia stipulata* occurred more locally towards the confluence of the Ludzi and Bua rivers.

'Other common trees in the miombo are *Uapaca kirkiana*, *Diplorrhynchus mossambicensis*, *Albizia versicolor*, *Strychnos pungens*, *Syzygium* sp., *Diospyros* sp., *Pseudolachnostylis maprouneaeifolia*, *Swartzia madagascariensis*, *Afrormosia angolensis*, *Dalbergia nitidula*, *Rostrhamnia taylorii*, etc. Trees occurring either very locally, or more rarely, were *Isoberlinia globiflora*, *Heeria insignis* and *Albizia antunesiana*.

'The transition from the miombo into either riverine, dambo or the *Combretum-Acacia campylacantha* woodland is abrupt and marked by the appearance of *Acacia macrothysa* and *Protea* sp. (Phot. 15) and the greater frequency of *Uapaca kirkiana* (Phot. 14). Looking across the Ludzi or the Bua river the miombo appeared as a wall of green woodland with a clear cut skyline uninterrupted by any larger trees.

'The wet dambos occur very commonly along the Ludzi valley but are less frequent along the Bua. They are treeless valleys clothed with six foot high grass growing on marshy clay soil. The dambos are usually only two to three hundred yards wide and wind far into the land bordering the rivers. They are not as wet as those seen on the Northern Rhodesian plateau land near Abercorn.'

#### 9. DOMIRA BAY, NYASALAND

'The higher summits of the escarpment between 5000 and 6000 ft. are clothed with *Brachystegia floribunda* and *Isoberlinia paniculata*. Descending from 5000 to 3500 ft. we pass into woodland of *Brachystegia microphylla* with *Brachystegia bussei* occurring as pure stands on red soil ridges. The poorer soil area are clothed with *Brachystegia longifolia*, *Brachystegia utilis* and a certain amount of *Brachystegia spicaeformis* and *Brachystegia burttii*. From 3000 to 2000 ft. the woodland becomes dominated by *Brachystegia burttii* on quartz gravel ridges, with *Brachystegia longifolia* common. Here the grass is scanty.'

'The *Brachystegia* woodland of the plains and low ridges at the foot of the escarpment lies between 2300 ft. and the Lake level (1500 ft.). It occurs on interfluvial ridges running eastwards from the scarp, and fading out into the *Combretum* association east of it. It also occurs as an island of approximately ten square miles in the area north-east of Nakondwa estate, and along the Rifu-Salima hill ridge (Phot. 50). This vegetation type is composed of *Brachystegia longifolia*, *Brachystegia spicaeformis*, *Terminalia sericea*, *Monotes engleri*, *Pterocarpus angolensis*, *Diplorrhynchus mossambicensis*, *Diospyros mespili-formis*, etc. The soil is of a reddish sandy consistency often charged with quartz debris and clothed with poor grass growth.'

#### 10. THE CENTRAL PROVINCE

'No one journeying along that part of the great north road which passes between Kondoa Irangi and Babati can fail to express admiration for the magnificent forest that clothes the Berekuru ridge. The well graded road winds

over pleasantly undulating grassland clothed with gigantic, flat topped, cedar like trees of *Brachystegia microphylla* some of which must be 80 ft. in height with a girth of close on 5 ft. (Phot. 11). The trees are so old that they have developed a coarse reticulate bark quite different from the smooth and flaking bark of the younger trees, or those found on the rocky hills already discussed. These great trees are festooned with pale green "old man's beard" lichen (*Usnea* sp.). Other plants associated with this forest are *Albizia antunesiana*, *Vitex cuneata*, *Acacia macrothysrsa* with its enormous leaf, *Brachystegia utilis*, *Dombeya quinqueseta* and *Combretum gueinzii*. The grass growth is excellent, being co-dominated by *Panicum maximum* and *Hyparrhenia rufa*, while in the spring when the grass is still short there is a wealth of flowers such as the blue *Thunbergia* and *Smithia*.

'Grass fires are a regular feature of this forest, keeping it free from undergrowth. However, in the shelter of rocks or ravines we find small evergreen thickets of *Rhus glaucescens* and *Myrsine africana* which shelter seedlings and saplings of *Podocarpus gracilior* that have germinated from seed brought by birds from the forest remnants on Salanga hill, and are attempting in vain to resuscitate what countless thousands of years ago must have been a great ridge of evergreen forest.

'The soils are exceedingly deep and of a rich terracotta red colour; erosion takes place very slowly and is not much in evidence.'

Apart from this *Brachystegia microphylla* of the highland plateau, and of the rocky kopjes previously described, 'the Central Province miombo is almost entirely composed of *Brachystegia spicaeformis* and *Isoberlinia globiflora*, but among them there is always a scattering of other trees, such as *Albizia harveyi*, *Albizia amara*, *Albizia versicolor*, *Combretum zeyheri*, *Commiphora pilosa*, *Commiphora fischeri*, *Ostryoderris stuhlmannii*, *Dalbergia ochracea*, *Dalbergia nitidula*, *Pterocarpus angolensis* and *Terminalia sericea*. Termite mounds are not common but where they appear one is almost certain to see the tall dark green "candelabra" *Euphorbia bilocularis*, perhaps a thickety shrub of *Commiphora stuhlmannii*, and very rarely a baobab.

'The Central Province miombo is comparatively poorly grassed, mainly with a small form of *Panicum maximum*, *Andropogon shirensis*, *Pogonarthria falcata*, *Eragrostis superba*, in places spear grass *Heteropogon contortus*, the red fluffy flowered *Rhyncheletrum roseum* and *Aristida adscensionis*. Flowering herbs feature commonly, especially varieties of *Crotalaria*, *Indigofera gyrocarpa*, the blue flowered Composites *Vernonia*, *Pycnostachys leptophylla* and various kinds of *Bidens*.

'The miombo along parts of the plateau above the Rift, at Kazikazi and Manyoni is almost entirely devoid of grass; flowering herbs grow among the leaf litter in the rainy season but in the dry season form insufficient kindling for the grass fires. Everywhere are fallen branches, torn from the trees by elephant, lying for years until they are finally removed by termites. Thickening

due to the absence of grass fires does not appear to take place even in the ages, and the scrub of *Herminiera glutinosa* which grows here and there can hardly be looked on as thicket.

'The rocky Saranda scarp, the scarp facing the Hika and Ruwiri rivers, and the prominent hills such as Mabora, Kunguye, Ikonze, etc. support large trees of *Brachystegia microphylla* of similar appearance to those of the Sambala hills, the Simbo hills and the Kikori escarpment of Kondoa District, with *Sterculia quinqueloba* and the small tree *Dichrostachys glomerata*. In these woods there is great regeneration of *B. microphylla*; on the steep slopes *Commiphora kymbillensis* is very common.

'Normal *Isoberlinia-Brachystegia* dominates a large part of the plateau [above the Rift Wall], *Isoberlinia globiflora* and *Brachystegia spicaeformis* being the commonest species. *Pterocarpus angolensis* is also very common, while in certain areas are very large trees of *Swartzia madagascariensis* and *Afzelia quanzensis*, and the shrub *Ximenia caffra* is very frequent. The miombo wooding on the summit of the scarp extending north-west towards Ndalambe and Mbukwa has a very clean and open appearance giving good visibility; the absence of coppice or shrubs is remarkable. Near Manyoni *Isoberlinia-Brachystegia* of a peculiar dry type resembling the woods of Kazikazi was seen, in which the peculiar small evergreen coppicing shrub *Teclea fischeri* and the spectacular evergreen cushion-forming Acanthaceous plant *Leptactinia benguillensis*, both common at Kazikazi, are very frequent.

'Near Hika and Ndalambe and along the scarp facing the Hika river, the *Brachystegia* woods contain a large quantity of shrubs and woody scrub that in places form small thickets in which the following plants are noticeable: *Herminiera trigonocarpa*, *Burttia prunoides*, *Cassipourea mollis*, *Ochna stuhlmannii*, *Vangueria* spp., *Teclea*, and in places a few plants of *Pseudoprosopis fischeri*. On the Hika scarp *Justicia salvioides* and *Acalypha fruticosa* form a fairly thick tangle of scrub. On the western side of the plateau, termite mounds were frequent in the *Brachystegia* wooding. These mounds were up to 12 ft. in height and clothed with thicket composed of *Capparis kirkii*, Rutaceous shrubs, *Commiphora stuhlmannii*, *Croton polytrichus*, *Grewia bicolor*, *Ochna stuhlmannii*, *Dalbergia stuhlmannii*, and a remarkable shrubby *Gardenia* bearing a waxy white flower smaller than that of *G. thunbergia*, and exquisitely scented.

'It was noted that the dry types of *Isoberlinia-Brachystegia* woods and those areas containing thicket seemed to have been very scantly burnt by the grass fires, and probably support a very thin herbaceous canopy, contrasting strongly with the eastern areas of the plateau that are cleanly burnt by the annual grass fires.

'At Kazikazi the miombo woods may be divided into two distinct types, dry *Brachystegia* woods and normal *Isoberlinia-Brachystegia*. The dry *Brachystegia* woods are found immediately adjacent to the deciduous thicket (Phot. 39) and are peculiar for the apparently complete absence of *Isoberlinia*.

*globiflora*. There are evergreen shrubs, but the herb stratum is extremely poor and unburnt by the seasonal grass fires. Elsewhere, in the normal woodland, *Isoberlinia globiflora* is a conspicuous co-dominant, and the herb and grass stratum is relatively richer. At Kazikazi this woodland is found at a lower elevation than the dry *Brachystegia* woods; and it is very much richer in species.'

In the eastern part of the Central Province, near Mpwapwa, '*Isoberlinia-Brachystegia* woodland clothes the major portion of the mountain slopes from 3800 to 5500 ft. (Photo. 12). On some slopes the magnificent cedar like tree *Brachystegia microphylla* dominates in places, but does not attain the splendid proportions of those on the Berekü Ridge, Kondoa District. The large and interesting tree *Brachystegia bussei* was seen on the higher slopes of Kiagaia and Luamba. It is common above Kikombo. *Brachystegia spicaeformis* is most characteristic of the Mpwapwa miombo woods except in the forests between Tubugwe and Mpwapwa where *Brachystegia boehmii* dominates, a species common in the Kilosa hills [further east] and in the Uluguru mountains [Morogoro]. The yellowish-white barked tree *Albizia tanganyicensis* is common in the lower *Brachystegia* woods together with *Acacia macrothysa*. Trees of *Lannea schimperi* are generally distributed and at Tubugwe reach a larger size than I had ever previously seen elsewhere. On the forest-hills of the Kiboriani block the large spreading tree *Sterculia quinqueloba* occurs sparsely, while a rocky ridge that traverses the *Isoberlinia-Brachystegia* woodland of that hill is clothed with open deciduous thicket in which the clean grey fluted trunks of *Commiphora kyimbilensis* (Phot. 33) are common. Rare species are *Commiphora ugogensis*, *Bauhinia petersiana*, *Holarrhena febrifuga* and *Pteleopsis* sp.

'Shallow drainage valleys traversing parts of the *Isoberlinia-Brachystegia* plateau between Tubugwe and Mpwapwa creek support occasional trees of *Acacia hebecladoides*, with *Dombeya quinqueseta*, *Combretum gueinzii* and *Combretum zeyheri*.

'The extensive dry *Isoberlinia-Brachystegia* woodlands which are so familiarly associated with the western and the northern parts of the Central Province (Phot. 9) are not seen at Mpwapwa, where the miombo woodlands have the general aspect of the forests of Kilosa and the Berekü Ridge (Phot. 11), in which large trees form the well grassed woodland in which little or no thicket is to be seen except in a dry watercourse or ravine.

'The Central Province *Isoberlinia-Brachystegia* woodland has a soft sandy soil of buff or slightly reddish tinge when dry. The subsoil at 2 or 3 ft. is hard when dry, and at 4 to 6 ft. lie nodules of iron concretions. The soils are of an acid type, and much sand is washed from them where they are traversed by roads.'

### 11. THE EASTERN PROVINCE

'The eastern or Kilosa type of *Brachystegia* woodland occurs on the Tubugwe hills east of Mpwapwa, the hills above Kilosa, between Kanga mountain and Handeni, and along some of the lower slopes of the Uluguru mountains at Morogoro (Phot. 13).

'This is essentially a miombo of the hills which are often steep. The trees are from 50 to 60 ft., and the long feathery leaves of the *filiformis* variety of *Brachystegia boehmii* are seen everywhere, paler and more shiny than those of the typical *B. boehmii* of the Kahama-Tabora miombo.

'A small leaved *Acacia* (*A. ulugurensis*) is commonly seen, with its very dark brown bark; and there are large trees of *Sclerocarya birrea* var. *multifoliolata*, *Albizia versicolor*, and *Brachystegia bussei* with smooth grey, flaking bark, and few and very pointed leaflets coppery in their first flush.

'This type of miombo is subject to greater rainfall than that up-country and consequently in the wet season contains exceedingly tall grass, *Hyparrhenia* and *Panicum maximum* growing to 6 or 7 ft. and discouraging the explorer.

'In the rainy season game spoor is not much in evidence, but paths of greater kudu, sable and zebra may be seen.

'The soils are composed of a sandy loam heavily charged with mica flakes derived from the mica schist underlying them. These soils are heavily eroded, partly because of the steepness of the hillsides.'

### III. THORN SAVANNAH: DECIDUOUS *ACACIA* AND *COMMIPHORA* TYPES

#### 1. THE LAKE AND CENTRAL PROVINCES

##### A. *Types on hard pan soils*

As the thornbush types are poorly represented in the miombo areas to the west and south (except in the Usangu plains of Mbeya District), it is most convenient to consider first the many types common to the Lake and Central Provinces, before proceeding to the description of the remainder.

'Just as the *Combretum* savannah woodland (see below, p. 111) on reddish soils is a feature of the higher ground, the hard pan country is a feature of the grey soil valleys on the lower slopes. As suddenly as we came out of the deciduous thicket into the miombo or the *Combretum* woodland, so do we pass out of the broad leaved *Combretum* with long grass and enter the open thornbush country of the hard pan, with its shorter grass and decorative flowers.

'If in a dry spell we try to dig up some attractive plant in the hard pan, we are amazed at the hardness of the grey soil composing it; but if on the other hand we try again after a tropical shower of rain has fallen, we find that one digs into soft soil of an almost buttery consistency to a depth of a foot or so,

when again we strike a layer with the hardness of concrete, and so dry that sparks fly as we dig. For this reason and for lack of a better term we call this country hard pan; these hard pan areas fringe the black cotton soils of the "mbugas".

(i) *Commiphora schimperi-Lannea humilis.*

This type of vegetation occupies the lower ground and valleys. It is widespread in the Lake and Central Provinces.

'The Shinyanga hard pan (Phot. 17, 19) looks at its best in January, when we find a wealth of flowers scattered over the short greensward of the glades. They are mostly the *Freesia*-like *Gladiolus grantii*, the white stars of *Lapeyrouisia* borne on long slender tubes, groups of the primrose-yellow *Gladiolus quartianus*, all manner of small squill like flowers (*Chlorophytum*), yellow spikes of ground orchids (*Lissophilus* sp.), a great variety of small vetch-like *Indigofera*, the bright pink and white blossoms of *Rhamphicarpa montana* and everywhere carpets of the little violet like flowers *Craterostigma hirsuta*. At Kazikazi in the Central Province the hard pan becomes carpeted with a delightful little blue *Gladiolus* reminding us of bluebell woods at home; here and there we see "red hot pokers" (*Kniphofia*) and down by the stream the large flower heads of *Crinum* sp.

'All these flowers and a great many more grow among the dwarf grasses *Microchloa indica* and *Sporobolus* sp., the fragile flowers of the latter forming in their legion a waving coppery sheen throughout the glades. These last may be as much as several hundred yards in length and twenty in breadth; they may be fairly straight following the drainage or they may form an intricate maze between the scattered thickets; they may be devoid of trees altogether or with small scattered trees of *Lannea humilis* (Phot. 18), *Commiphora schimperi*, *Dalbergia melanoxylon* the "African ebony", and dotted about in them an odd *Acacia drepanolobium* or even a few larger trees such as *Sclerocarya birrea* var. *multifoliolata*, *Terminalia stuhlmannii*, *Acacia tortilis* and *Acacia rovumae*, and the feathery leaved Albizzias, *A. harveyi* and *A. amara*.<sup>1</sup>

'Along the margin of the glades we usually see small groves of *Lannea humilis*, whose silvery grey trunks in the dry season suggest orchards of apple trees, and whose bark is used for rope by the natives. Everywhere are green barked small trees of *Commiphora schimperi*, with resinous scented sap, growing up to 12 ft. in height and used by the native for live pole fences for his cattle "boma". On every hand are small thickets clustered round termite mounds, from whose greenness rise the flat topped crowns of *Terminalia stuhlmannii* or the rounded tops of *Acacia nigrescens*, *Commiphora stuhlmannii* and the occasional baobab.

'The wetter parts of the hard pan may be carpeted with a prickly mass of *Blepharis acanthoides* with pretty blue flowers, or the round white "hat pins" of sedges, *Kyllinga alba*.

<sup>1</sup> And the smaller *Acacia mellifera*.

'In December the margins of the small thickets will be gay with the yellow flowered shrubs *Grewia bicolor*, *Grewia fallax* and an unidentified species, the white blossom of *Dombeya* sp. and the tall orange spikes of Aloes. Other hard pan trees and shrubs are *Royena fischeri*, *Acacia senegal*, *Combretum parvifolium*, *Hymenodictyon parvifolium* and *Rothmannia taylorii*.

'With the late rains, most of the hard pan becomes choked with tall swathes of *Hyparrhenia rufa* 3 to 4 ft. in height, with *Cynodon plectrostachyum*, *Cenchrus ciliare* and *Bothriochloa insculpta* on the wash from termite mounds.

'In the dry season fires burn through the hard pan, destroying the suckers of *Dichrostachys glomerata*, *Commiphora schimperi* and *Ornocarpum trichocarpum* which have been growing up among the grass, and, were fires excluded, would soon grow up to form a thorny tangle impenetrable to man (Phot. 37).

'The hard pan is a favourite haunt of game. Giraffe come out of the *Combretum* and miombo woodland to feed on the leaves of *Commiphora schimperi*. Herds of impala are frequently seen, and sometimes in the dusk greater kudu. In the hard pan below the Singida Rift Wall, we see in the morning fresh spoor of rhinoceros which have been feeding on the *Lannea humilis*, and in the dry season the well worn paths of elephant leading down to water. Because of their openness the hard pan valleys are much used by game in their wanderings; there are in the dry season always a number of game trails leading up and down the valleys following the glades, and it is to such places that the hunter goes to look for game.

'The soil is of a grey colour, setting hard in the dry season and not cracking. In the rains it becomes soft at the surface—the clay nature of the soil causes it to be slow in absorbing water. The depth varies from 2 to 15 ft.; the subsoil is highly calcareous and may rest on granite bedrock.

'The hard pan thickets may be only small clumps of *Combretum parvifolium* encircling an isolated tree of *Commiphora schimperi* or *Lannea humilis*; or they may be from 10 to 100 yards in diameter. The larger thickets near Shinyanga contain much *Anisotes dumosus*, a dark leaved shrub growing to 8 ft. in height. From among the *Anisotes* grow the green stems of *Commiphora subsessilifolia* and the rounded tops of *Commiphora stuhlmannii*, over which may be draped that grey, serpent-like climber *Fockea schinzii*, *Combretum purpureiflorum* bearing masses of scarlet blossom in the late dry season, or the "barbed wire" Capparid, *Capparis elaeagnoides*.

'Other plants which are commonly found in the hard pan thicket are *Albizia harveyi*, *Albizia amara*, *Acacia nigrescens*, *Acacia rovumae*, *Balanites tomentosa*, *Commiphora sarandensis*, *Boscia fischeri*, *Dalbergia ochracea*, *Teclea glomerata*, *Dichrostachys glomerata*, the thorny and knobbly barked *Fagara merkeri* whose leaves emit a strong scent when crushed, the robust *Mimusops densiflora*, *Maerua angolensis*, the thorny tree *Ziziphus mucronata* and the scrub *Cadaba adenotricha*.

'In the Central Province hard pan thicket we may see the pale blue-green



Phot. 11. Magnificent woodland of *Brachystegia microphylla* on the Bereku Ridge north of Kondoa Irangi, at about 5000 ft. (pp. 83, 85). (Photo by W. H. Potts.)



Phot. 12. The miombo of the Mpwapwa hills (middle distance) looking towards Dodoma. In foreground, the *Protea* zone above the miombo can be seen (pp. 85, 116, 117).



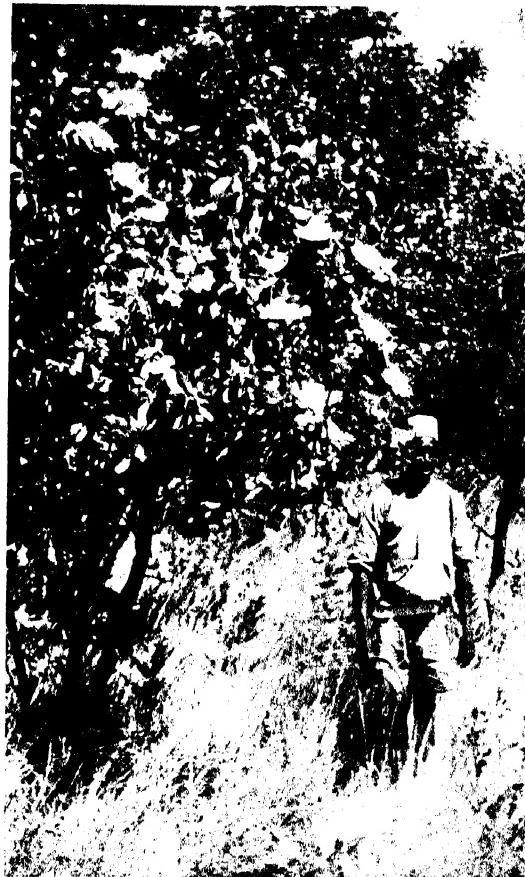


Phot. 13. Miombo woodland near Morogoro (p. 86).



Phot. 14. *Uapaca* sp. in an open space among the Abercorn miombo (pp. 79, 82).





Phot. 15. A pink flowered *Protea* near Abercorn (pp. 79, 116).



Phot. 16. *Acacia burtii* in a valley in the Kah miombo. Note the spherical white flowers, and gall at the base of each pair of thorns, best towards the bottom of the picture (p. 98).





Phot. 17. Typical short grassed hard pan in Shinyanga; early dry season. *Commiphora schimperi* group in centre, and a single *Acacia nigrescens* in left background. The thickets are mostly *Combretum parvifolium* (p. 87).



Phot. 18. Gall-acacias (*Acacia formicarum*) on left, and *Lannea humilis* in centre, where the hard pan meets the heavier, cracking soil; again dry season aspect, after poor and patchy fire (p. 87).





Phot. 19. Hard pan in Shinyanga, with a grove of *Lannea humilis*, in the rainy season; note the short grass (p. 87).



Phot. 20. A typical *Acacia mellifera* in short grassed hard pan.  
Note the bun-like canopy (p. 90).





Phot. 21. Open savannah of *Acacia roruma*, a baobab and *Euphorbia bilocularis* (right), with thickets of *Combretum parvifolium*. Hard pan in Singida, near the Wembere Steppe (p. 90).



Phot. 22. *Acacia roruma* savannah in Maswa, with rather long grass.  
Note the fluted trunks (p. 90).



coloured trunks of *Commiphora caerulea*, or outside the thicket a spiny margin of the remarkable plant *Commiphora stolonifera* and the blue flowered aromatic succulent Labiate, *Coleus ignarius.*'

(ii) *Acacia drepanolobium.*

This species is widespread in the Lake Province, and is noticeable in the Central Province in the Bubu valley, the Rift Valley and in the Masai Steppe.

'In our way through the *Commiphora-Lannea* hard pan country we have seen scattered groups of gall-acacia, *A. drepanolobium*, usually in the glades; they are spindly trees mostly from 6 to 10 ft. in height with short branches radiating from the main stem. Where the grass fires have been less severe the gall-acacias grow with a spreading habit; in fact, the severity of the grass fires determines their shape, the flames pruning off the lateral twigs which are within their reach. The dark brown or almost black galls the size and shape of chestnuts and armed with two white needle-like thorns grow all along the twigs and branches, giving the tree a peculiar appearance (Phot. 28). Each gall is pierced with a little hole made by small black ants when it was soft and young, and the gall is inhabited by the ants and full of their small white grubs and pupae. Should one try to pick a branch or even jar it, out come the ants fussing about all over the twigs and ready to bite anything that arouses their suspicion.'

'As we descend the ever broadening hard pan valley we often find that its floor flattens out into a more or less broad plain, supporting a veritable forest of gall-acacias to the exclusion of everything else except an occasional hard pan thicket clustered round a termite heap. The gall-acacias may grow so close together that we are unable to pass through them; or on the other hand along the edges of "mbugas" the trees may rise to 20 ft. in height, their scraggy appearance and tall single trunks being almost sinister. A passing breeze at once sets up a shrill whistling, caused by the wind blowing over the little holes in the galls and giving rise to the popular appellation of "whistling thorn".'

'In February the *Acacia drepanolobium* are covered with sweet-scented small white flowers and the branches are decorated with pale bluish-green leaves. The ground is either carpeted with a spiny growth of *Blepharis acanthoides* or covered with slender grasses such as *Aristida steudeliana*, *Aristida adscensionis*, *Microchloa indica*, *Sporobolus* sp., *Cenchrus ciliare* and *Cynodon plectrostachyum* on the wash from termite mounds.'

'The soil is very similar to that of the *Commiphora-Lannea* described above, except that the surface is often bare and covered with a sandy rust.'

(iii) *Commiphora campestris.*

'This tree is confined to the neighbourhoods of Lake Natron in the Northern Province and of the Wembere Steppe between the Lake and Central Provinces, and parts of its extension, the Manyonga basin.'

'If we proceed by road from Mkalama to Sekenke round the foot of the Iramba scarp, or from Shinyanga towards the Wembere Steppe, our attention is drawn to the olive green or pale blue-green foliage clothing extremely grotesque and knobbly trees of *Commiphora campestris* which are to be seen everywhere. If we pause to investigate them and do not take care, we are soon caught up by twigs of *Acacia mellifera* (Phot. 20), the "wait-a-bit" thorn, a small, bright green, bun-shaped tree from whose lacerating grip we extract ourselves with caution. Grass is almost absent and the soil sandy and nearly bare. In glades we see the small shrubby *Acacia orfota* (Phot. 26), whose green bark gives off an obnoxious smell when cut. Everywhere are scraggy plants of *Euphorbia matabensis*, a small tree resembling a *Commiphora* as its bark also peels off with papery shavings. It has a remarkable zigzag branching caused by its twigs growing out in threes. Natives manufacture birdlime from the milky sap.'

'Low termite mounds are scattered about, clothed with shrubs of *Anisotes dumosus*, and the slender scrubby plant *Maerua trichophylla* round which almost always flit a few small orange-tip butterflies. Fleshy creepers such as *Cissus quadrangularis* and *Cissus rotundifolia* drape themselves over the shrubs and large green leaved Aloes are common.'

'Even in the rains the soil is hard and firm and easy to motor over; but care must be taken during showers, as the surface of the ground is immediately covered with a film of vaseline like mud which transforms the hard even surface into a skating rink.'

'In the dry season, grass fires are unable to penetrate much of the *Commiphora campestris* hard pan, a fact which enables peculiar spiny succulent Euphorbias and Aloes to persist.'

'Impala and dikdik are common, and also guineafowl, lesser bustard and flocks of sandgrouse.'

'The soil is very like that of the *Commiphora-Lannea* hard pan already described; but the slippery crust formed when wet appears to prevent the percolation of water to any appreciable depth, with the result that the soil soon dries and sets hard again.'

#### (iv) *Acacia rovumae*.

In the Central Province this is found in the Bubu, Ruaha, Rift Valley and Wembere drainage systems (Phot. 21). In the Lake Province it is widespread. It extends southward to the plains of Usangu and the Rukwa depression in Mbeya, and is scattered through the Tabora miombo.

'As we pass through the *Commiphora-Lannea* country we see from time to time large flat topped *Acacia* trees which at first we take to be *Acacia tortilis*, but on closer inspection we perceive their fluted trunks (Phot. 22), small hooked thorns, and, in July, the spikes of yellowy-white flowers that cover the trees as if with a blanket. These trees are *Acacia rovumae*, which in certain

areas grow in large numbers forming a distinct woodland type, sometimes fairly open, sometimes filled with such a dense tangle of shrubs as to be impenetrable.

'In more open woodland we find *Commiphora schimperi*, *Lannea humilis* and the occasional *Acacia senegal* growing in the grassy glades; or small island thickets of *Grewia fallax*, *Grewia similis*, *Grewia praecox*, *Ehretia caerulea* and *Combretum parvifolium*. In these thickets are usually succulent vines *Cissus quadrangularis* and *C. rotundifolia*, while the grass around them forms an almost pure carpet of *Cynodon plectostachyum* that trips us up at almost every step. Taller grass, *Panicum maximum*, grows in clumps under the larger trees, together with the herbs *Monechma bracteatum*, *Vernonia poskeana* and *Achyranthes aspera*. In the denser woodland the grasses may be more or less excluded by the shrubby tangle composed of *Anisotes dumosus*, *Opilia campestris*, *Commiphora stolonifera* (in the Central Province), and the "asbestos weeds" *Blepharis*, *Barleria* and *Disperma* which will not carry fires in the dry season.'

'Eland, impala, roan and hartebeest are fond of lying up in open *Acacia rovumae* woodland. In the Rift Valley the denser woodland is a favourite resort of rhino whose maze of paths through the thickety tangle makes progress through them easier than one would have expected.'

'The soil appears to be very much of a hard pan type.'

#### (v) *Acacia fischeri*.

This type occurs locally in patches or groves in hard pan country throughout the Lake Province, more rarely in the Central and Western Provinces.

'As one passes through the broad expanses of hard pan country the route will often lead across drainage glades clothed with very short grass and groves of *Acacia fischeri* trees whose foliage is exceptionally long and feathery and of a bright green colour, and whose stems have dark brown and deeply furrowed reticulate bark. These trees are usually about 10 ft. in height with a flattish crown, but sometimes the older ones grow to 20 ft. and carry a more regular canopy. The orchard-like groves of *Acacia fischeri* are frequently met with as a broken fringing strip 20 to 80 yards wide on the flood plains of large seasonal rivers such as the Simiyu in Maswa, but generally they are limited to small groves a couple of hundred yards long in shallow drainage glades.'

'The soil is similar in appearance to the soil of the *Commiphora-Lannea* community, but may be saturated for longer periods. It is a poor soil for crops, and where stony useless.'

#### (vi) *Acacia usambarensis*.

'Also found locally between the riverine and the *Commiphora-Lannea* type of hard pan country, but not often seen in the Central and Lake Provinces, it is however very common in the eastern areas such as the Wami plains and the

foot of the Usambara mountains. It is seen in Maswa near the Simiyu and at Kikori at the foot of the Bereku ridge in Kondoa District.

'Travelling up the Tanga line the train crosses the flats at the mouth of the Lwengera valley before entering Korogwe station, and the traveller gazes up the steep sided rift which severs the eastern from the western Usambaras. Before him lies the rich open grassland studded with a forest of dark green leaved Acacias whose canopies are noticeably rounded and balloon shaped. These are *Acacia usambarensis*, the "stink bark acacia", a tree growing to 50 ft. in height and with bark that at certain seasons gives off a powerful and unpleasant odour when injured, as when collected by the native for string which he uses for tying together the framework of his house.'

'*Acacia usambarensis* woodland covers extensive areas of the Wami plains west of the river, and we pass through it on our journey from Morogoro to Turiani and Kilosa; in this area the Acacias are interspersed with *Combretum imberbe*. The forest is fairly well grassed, and the absence of thickets testifies to the fierceness of the grass fires.'

'Up-country, *Acacia usambarensis* woodland is scarce, one typical area being on the flats below Kikori village, north of Kondoa Irangi, where the woodland is localised on the sandy wash from the *Brachystegia microphylla* escarpment above. The second area lies north of the Simiyu river in Maswa District (Phot. 23), where extensive stretches of this woodland grow on the reddish soils of the gently undulating country facing the river.'

'On the lower slopes the grasses are chiefly composed of *Panicum maximum* under the trees, with *Cynodon plectostachyum* in the glades, in which grow a profusion of decorative herbs such as *Monechma bracteatum* and *Vernonia poskeana*. On the higher ground we find that the herbage is dominated by a pure stand of *Hyparrhenia rufa* averaging 4 ft. in height.'

'The *Acacia usambarensis* woodland occurs usually on the lower valley slopes near the river, where the soil must contain a good deal of wash from the higher slopes; in general appearance it resembles that of the *Commiphora-Lannea* type. In riverine areas the soil is of a more sandy nature. It is good for crops.'

#### (vii) *The fan-slope type of hard pan.*

'This occurs on grey soil areas localised around the foot of granite hills in Usukuma, as for example at the base of the Kimali hills in Maswa District, between the granite hill and the *Combretum zeyheri-Ostryoderris-Commiphora fischeri* woodland, which covers most of the higher ground on which the kopjes occur.'

'These fan slope areas have mixed vegetation, containing large and scattered trees of *Acacia usambarensis*, *Acacia rovumae*, *Acacia tortilis* (Phot. 35) and *Lannea stuhlmannii*, and small trees of *Acacia senegal* and *Commiphora schimperi*, and *Acacia holstii* more rarely. Here and there are small groups of

gall-acacia (*Acacia drepanolobium*) and island thickets of *Grewia fallax*, *Royena fischeri* and *Anisotes dumosus*.

'The grasses of the fan slopes are richer than in the *Acacia fischeri* or *Acacia drepanolobium* hard pan valleys, being mainly *Cynodon plectrostachyum*, *Cenchrus ciliare* and *Themeda triandra* growing to 1½ ft. high. Looking down the fan slope, we see that it suddenly changes into the *Combretum-Ostryoderris* woodland, whose tall *Hyparrhenia rufa* grass, 3 to 4 ft. high, stands out like the edge of a field of corn.'

'The soil resembles those of the *Commiphora-Lannea* and *Acacia drepanolobium* hard pan types mixed up in a mosaic complex.'

(viii) *Acacia tortilis* (= *A. spirocarpa* Hochst.).

'This type is to be found in the Shinyanga area especially in the south and in large tracts of country bordering the Wembere Steppe; in the Rift Valley; in the Masai Steppe in the neighbourhood of the Irangi escarpment; and southward to Mbeya in the Usangu plains (Phot. 24) and the Rukwa depression.

'Of all the woodland types in East Africa the *Acacia tortilis* woodland is the best known, as it so often forms the background of game cinematography. We are shown elephant among these flat topped *Acacia* trees, herds of zebra, wildebeest, oryx and Grant's gazelle dallying by the waterhole in their shade, and sometimes the stately giraffe with slowly switching tail.'

'The traveller in Tanganyika will however find that *Acacia tortilis* woodlands are few and far between, and he will have to go far from the beaten track to find them. Nowhere can this magnificent woodland be seen along either the Central or the Tanga railways, and he must go by car or by foot to the edges of the great plains of Masailand, the Serengeti or the Wembere, where these forests and where game of all kinds abound.'

'*Acacia tortilis* woodland is definitely a parkland, often very open. The grasses form rich and unrivalled grazing, being largely *Cynodon plectrostachyum* in the open and *Panicum maximum* among the trees. In the dry season the grass fires are fierce and burn out most regenerating shrubs, while ash covered ground below the trees becomes littered with the twisted *tortilis* pods, that bring eland and impala to feed upon them.'

'Away from the great plains, *Acacia tortilis* woodland of less extent will often be found fringing seasonal rivers such as the Bubu in Kondoa, the Tubugwe-Matamondo rivers of Mpwapwa and the larger rivers that flow westwards into Lake Victoria.'

'The soil is a grey sandy clay setting hard in the dry season. It may be rich in alluvial sand and silt when near rivers, and is usually good for crops.'

*Acacia benthamii* is a common tree of this type, and also of *Combretum* savannah in Shinyanga.

(ix) *The thornbush elements on stony hills.*

'This is the characteristic type on hills of banded ironstone, dolerite, coarse schists and quartzite, as in parts of the Lake Province, parts of western Kondoa and the Iramba escarpment, and volcanic hills in Mbulu District of the Northern Province.

'In parts of the Central and Lake Provinces the flat skyline of hard pan country is broken by low rounded hills rising like a whale back to several hundred feet out of the horizon. Sometimes the hills are composed of coarse blocks of banded ironstone, while others seem to be entirely made up of quartzite pebbles. If we scramble up these hills we find that they are often clothed with a peculiar tufted grass *Sehima nervosum* interspersed with "spear grass", *Heteropogon contortus*. Stunted, semi-flat topped Acacia (*A. hebecladoides*) will be seen commonly, a species which we did not see in the flat country round the hills. Here and there may be tall, round topped trees of *Acacia nigrescens* and *Acacia goetzii* with broad leafy pinnules; the slender *Acacia holstii* with small yellow flowers and scaly bark is also frequent, together with the bright green leaves of *Combretum ghasalense* (Phot. 32). Scattered over the hill will be various hard pan elements such as *Ornocarpum trichocarpum*, *Lannea humilis*, *Fagara merkeri*, *Grewia bicolor* and the "African ebony" *Dalbergia melanoxylon*.

'In the dry season the hills are swept by grass fires revealing their stony surface almost devoid of soil, which has been dashed by a millennium of rainy seasons into the fan slopes which surround their bases.'

Such soil as remains 'is bright reddish, occurring in small pockets or as a "skeleton soil" among the rocks. It is quite useless for agricultural purposes. However at the base of the hills a red soil of considerable depth has been formed that is fairly good for crops.'

B. *Types on seasonal swamps*

'If we climb a hill which is high enough to enable us to look out over wide areas of country, our attention is usually drawn to an area of open grassland devoid of trees, its sinuous margin as sharply defined as the shores of a lake. We notice that these open grassland areas are usually in low lying country and vary in size from a few hundred yards in length to areas often covering many square miles (Phot. 31). From the Berekü ridge in northern Kondoa, we see these great "mbuga" systems reaching far out into Masailand; or, if we fly by aeroplane from Singida to Shinyanga, we see the grassland of the Wembere Steppe extending far towards the southern horizon and northwards towards Lake Eyasi. West of Shinyanga we see the vast tracts of the Huruhuru "mbuga" fading into the western horizon and the Buhungukira hills. Similar open plains occur in Usangu and the Rukwa depression of Mbeya District; in

our travels by air over the Territory the patterns of "mbugas" become very familiar to us.

"To the motorist "mbugas" spell trouble in the rainy season, for the black soil of which they are composed has become a slippery mire in which the wheels are soon embedded axle deep. Often during the rains "mbugas" become impassable for several months, while in the dry season the black soil cracks deeply in drying, forming a bumpy surface over which cars must proceed with caution.

"During the dry season, "mbugas" become a favourite resort of plains game, especially eland, zebra, wildebeest, hartebeest and gazelles. With the rains these animals repair to drier ground.

"The treeless, completely open "mbuga" will be found in the rainy season to support rich pasture mainly composed of the tussocky grass *Setaria holstii*, which may be interspersed with *Digitaria regularis*, *Themeda triandra* and various flowering herbs such as the tall hollyhock-like *Hibiscus cannabinus*, and the yellow flowered Composites *Aspilia* and *Wedelia*.

"The soil is a dark grey-black clay, cracking deeply in the dry season and becoming very sticky when wet."

In the Lake and Central Provinces, the thorn trees of the 'mbuga' are nearly always one of four species of gall-acacia; west and south of the Lake Province, two other species of gall-acacia play a comparable role.

#### (i) *Acacia drepanolobium*.

This species has already been described in the last subsection (A (ii)), as growing on hard pan soils. However, especially where other species are absent, it does form pure stands of relatively tall trees growing close together in the heavy clay soils of the 'mbuga', as in the Huruhuru system west of Shinyanga and in parts of western Kondoa District. It is very widely distributed in the Lake Province especially, extending into Musoma District on the eastern side of Lake Victoria. (Burtt has omitted this species from the list of gall-acacias growing on 'mbuga' soils, implying that it is only found on the hard pan.)

#### (ii) *Acacia seyal*.

"These yellow barked gall-acacias [the form bearing galls is known as var. *fistula*; the typical form seems less common, but both may be found together] are very local but widely distributed in the Territory, and usually indicate areas which are subject to longer saturation during the rainy season. They are commonly found along the margin of the Wembere Steppe where large seasonal rivers run into it, in many isolated "mbuga" systems of the Central Province, in many of the "mbuga" systems of the Masai Steppe, and on the Usangu and Rukwa plains of Mbeya. [They often occur in company with the dark green leaved tree *Balanites aegyptiaca*.]

"As we gaze over the great sea of open "mbuga" our attention may be

directed to a small patch of woodland far away in the mirage of shimmering heat. As we approach this woodland we see that it is composed of trees 20 to 35 ft. in height, with bright yellow-orange bark, and twigs littered with porcelain-white galls the size of walnuts. These trees are *Acacia seyal* var. *fistula*, a species bearing bright yellow flowers. The *Acacia seyal* forest will be found to occupy the wettest part of the "mbuga" where the soil is waterlogged for a longer period; during the rains the bark assumes a greenish or greenish-yellow tinge.

'The soil is similar to that of the open "mbuga" but usually darker, becoming more waterlogged in the rainy season and remaining saturated for a longer period.'

(iii) *Acacia malacocephala*.

'The "gum-arabic" gall-acacia covers vast expanses of country fringing the Wembere Steppe and extending up some of the tributary valleys. A form of this community appears on the south Mbulu plateau in the Northern Province, in the neighbourhood of Lakes Basotu and Basodesh.'

'If we "safari" up and down the margin of the Wembere Steppe, we shall find that vast areas are clothed with spindly *Acacia malacocephala* trees with brown stems, growing 10 to 20 ft. in height, whose branches and twigs are covered with brown ant galls the size of chestnuts. In the dry season the trees are leafless, offering no shade to the traveller, while the lightest breeze among their branches produces the same peculiar whistling sound described under *Acacia drepanolobium* in the hard pan.'

'In the later dry season the trees are whitened with blossom that disappears in the first rains, when the trees become clothed with olive-green, feathery foliage. (The allied *Acacia drepanolobium* flowers in the rains.)'

'It is from these *Acacia malacocephala* trees that the bulk of the "gum-arabic" of commerce is collected in this Territory, the gum exuding in amber coloured tears from twigs that have been injured by boring insects, or damaged in other ways.'

'The soil appears to be similar to that of the open "mbuga" described above.'

(iv) *Acacia formicarum*.

'This is a feature of the margin of some of the large open "mbuga" systems in Masailand, especially those found along the base of the Berekuru ridge in Kondoa District. *Acacia formicarum* is also especially common in the upper drainages of the Kizigo and Kazikazi rivers, more locally on the south Mbulu plateau, and in the Singida District along the foot of the Rift escarpment (Phot. 29). It is also seen on the Kilimatinde plains, and in many places to the southward towards Mbeya.'

'This type covers very much more localised areas and is a feature of the



Phot. 23. *Acacia usambarensis* hard pan in Maswa; note the long grass (p. 92).



Phot. 24. *Acacia tortilis* savannah on the Usangu flats, Mbeya (pp. 93, 99).





Phot. 25. *Acacia keniouge* scrub on hard pan in Manyoni, very poorly grassed (p. 110).



Phot. 26. Loose thicket of *Acacia orfota* on hard pan at the edge of the Wembere Steppe; dry season (p. 90).





Phot. 27. *Acacia stuhlmannii* hard pan. This tree is often dominant in hard pan areas inundated for long periods in the rains; note very poor grass growth; dry season (p. 97).



Phot. 28. *Acacia kirkii* hard pan, with gall-acacia twigs in foreground, showing plainly the ant galls; very poor grass; dry season (p. 97).





Phot. 29. Gall-acacias (*Acacia formicarum*) in Singida; dry season after fires (p. 96).



Phot. 30. The gall-acacia of the southern miombo; *Acacia natalitia* in Nyassaland.  
Note the very elongate, white galls. Early dry season (p. 143).





Phot. 31. Open grassland of the Serengeti ash plains, with a vast herd of wildebeest, *Gorgon albojubatus* (p. 94).



Phot. 32. The Serengeti plains, Musoma. The higher ground is dominated by *Combretum ghasalense*; the acacias in the open space below are probably *Acacia hebecladoides*. Note the heavy forest on the seasonal stream, and thicketed termite mounds in open (pp. 94, 126).





Phot. 33. Thicket dominated by *Commiphora kyimbilensis* on the Lake Tanganyika coast below Abercorn (pp. 85, 104).



Phot. 34. Typical thicket in the Kimali hills, Maswa. Note the strongly fluted trunk of *Commiphora eminii*, bearing a nest of the hammerkop (*Scopus umbretta*) (p. 101).





Phot. 35. Hill thickets in Shinyanga, with savannah of *Acacia tortilis* on the fanslopes below (pp. 92, 101).



Phot. 36. Hill thicket in Mwanza, with a mango tree growing in the cleared cultivation steppe. Goats were excluded only from the nearer hill which shows the dark mass of regenerated thicket, in contrast to the open, paler hills behind (p. 101).





Phot. 37. Thicket of *Dichrostachys glomerata* in Singida, near the Wembere Steppe.  
In better grassed country these thickets are suppressed by fires (p. 88).



Phot. 38. Baobabs (*Adansonia digitata*) in the Shinyanga cultivation steppe.  
Note patches of native crops (p. 101).



smaller "mbugas" of the Central Province. The grasses are of the typical "mbuga" type, but the gall-acacia scattered about in them will be seen in the dry season to have a rusty-red powdery bark, especially on the twigs and younger branches which have not been so badly fire scarred.

'In the rainy season the long feathery leaf of fresh green colour will at once distinguish this gall-acacia from *Acacia drepanolobium* and *A. malacocephala* whose leaves are olive green.'

'Often the *Acacia formicarum* trees will be almost poles, 15 to 20 ft. in height with short stubby radial branches. This effect has to my mind been produced by the pruning action of grass fires and is also seen in other species of gall-acacia. Where the fires are less fierce the trees are more irregular and bushy.'

'The soil is similar to that of the open "mbuga", highly calcareous in the Kazikazi area.'

#### C. Types on flood plains and deltas

'Flood plain and delta deposits are very common along the rivers which flow into the Wembere Steppe, the Bubu and Mponde river systems, other parts of the Central Province and the Usangu plains in Mbeya.'

'Where seasonal rivers suddenly enter the flat plains of "mbugas" such as the Wembere or smaller "mbugas" along their course, the water in flood time spreads out over a broad sheet of country that is dissected by a maze of many small watercourses. During this flooding process, the fine clays are deposited, and in the dry season bind together into a stony hardness. In areas where the flood water has lain for some time in shallow pools the soil is almost black in colour, cracking deeply in the dry season; the soil in the drier areas is of a grey hard pan like formation that does not crack.'

'Most of this flood plain area is clothed with *Acacia kirkii* (Phot. 28), a tree growing to 15 or 20 ft. and with peculiar radial branching and a very short trunk often only 3 or 4 ft. in height. The bark is a yellowish-brown colour and peels with papery shavings, while the canopy is remarkably flat topped.'

'In moister areas of the flood plain, and clustered along the small water-courses, we find the small hairy *Acacia stuhlmannii* (Phot. 27) with exceptionally hard and hairy pods. The pools themselves support a growth of *Hygrophila spinosa*, which in the leafy season appears as an innocent green mass of herbage studded with white, dead-nettle like flowers, but which in the dry season becomes a mass of brown stalks armed with incredible spines.'

'The drier parts of the flood plain support small trees of *Maerua crassifolia*, *Commiphora subsessilifolia*, occasional *Acacia drepanolobium*, *Salvadora persica*, *Acacia mellifera* and *Commiphora stolonifera*, while occasional termite mounds may be guarded by a spiny mass of *Sansevieria robusta*. The flood plains are often flanked by *Acacia seyal* "mbugas" or by *Commiphora campestris* hard pan on the higher ground. As would be expected they are studded with seasonal pools, while the drier areas are almost devoid of grasses.'

## 2. TABORA

The only thornbush communities of importance in the Tabora miombo are *Acacia rovumae* on hard pan and three species of gall-acacia growing on heavy 'mbuga' soils.

The *A. rovumae* hard pans of the Tabora District occur as discontinuous strips or interzones, usually not more than 30 yards wide, between the margins of the *Isoberlinia-Brachystegia* woodland and the *Combretum-Afrormosia* or the gall-acacia 'mbuga'. The dominant large tree is *Acacia rovumae*, often with a mixture of *Terminalia sericea*, but numerous termite heaps support thicket and other large trees. *Lannea humilis* and *Royena fischeri*, and the shrubs *Hymenodictyon parvifolium* and *Combretum obovatum*, are all exceedingly common, and *C. zeyheri* and *C. ghasalense* are frequent.

The hard pan soil is covered with an often thick sandy wash from the miombo woodland above.

The heavy clay 'mbugas' are usually waterlogged for several months in the rainy season, and support a new species of gall-acacia probably related to *Acacia formicarum*, and like it flowering in the dry season. This gall-acacia has very long leaves of a rich dark green colour, contrasting with the deep purply brown of the younger branches. The galls support paired stumpy thorns which are never silvery (as they are on the other gall-acacias) except in quite young coppice.

In the north and east of the District, *A. formicarum* dominates in the 'mbugas', but 40 miles south of Tabora the new species replaces it as soon as the hilly country gives place to the great flat plateau.

Less heavy 'mbuga' types may support locally the fawny barked gall-acacia, *A. burttii* (Phot. 16). Of this species in Kahama District, where it is rather more frequent, Burtt writes: '*Acacia burttii*, with *Combretum ghasalense*, is found among the *Brachystegia* woodland. In the Kahama country, "mbugas" of brownish soil are frequently seen in the valleys, clothed with almost pure stands of this remarkable gall-acacia whose bark is of a buff or fawn colour and whose galls are speckled with little spots of red, brown or white. The flowers which appear in February are the largest found among the Tanganyika gall-acacias and are white in colour, while the short leaves are composed of stiff broad pinnules which are pointed and spiky. Often these "mbugas" are scattered with bright green small trees of *Combretum ghasalense*, kept stunted by the grass fires. Spoor of Lichtenstein's hartebeest and sable may be seen.'

'The soil is a deeply cracking light brown clay, exceedingly sticky in the rains.'

## 3. MBEYA

'Ten miles from Mbeya towards Iringa the road winds over the 8000 ft. volcanic massif of the Mporoto mountains and descends at mile 30 through *Brachystegia* woodland to the plains of Usangu. Before we leave the high

country of rolling grassland with scattered trees of *Parinari curatellaefolia* and *Erythrina abyssinica* we look away to the east along the escarpment wall of the Elton plateau whose lower slopes are clothed with *Brachystegia* forest. To the north we see the distant wall of the Mbeya escarpment fading away into the hazy distance towards Madibira, while below the countless tops of *Acacia tortilis* trees (Phot. 24) sink mistily towards the yellow grass line of the great "mbuga" or "balali" of Usangu.

'From mile 30 to the Ruaha bridge the motor road passes through the *Brachystegia* forest at the foot of the escarpment, but between the Ruaha and the Kimani river and six miles beyond that river the country is clothed with hard pan thicket containing *Acacia kirkii* and *Commiphora caerulea*; in this area the soil is of a pinkish-purple colour derived from shales which, where they outcrop, are clothed with *Commiphora ugogensis*, *Strophanthus eminii* and *Grewia* spp.

'The main feature of Usangu is the great "mbuga" called the "balali" by the natives. The "balali" at the time of my visit [October] appeared as a great grass plain, with reeds fringing water channels some of which were deep and filled with water. In the rainy season the "balali" is flooded by the Ruaha and becomes a huge lake whose tidemark can be seen as brown smears on the white trunks of *Acacia seyal* var. *fistula* which are common round the shores. Hippo, which are restricted to "ambatch" clothed pools of the main Ruaha during the dry season, wander far afield in the rains in their extended horizon.

'*Acacia tortilis* woodland seen from the hills apparently covers vast areas of Usangu on the south and eastern margin of the great "balali" and includes the principal grazing and cultivated areas. The trees form an almost pure stand on rich brown sandy loam which in places supports good grass growth but is in other areas clothed with a spiny and burly herbage of *Cyphocarpa* sp. (Amarantaceae).

'The hard pan *Commiphora-Acacia* thornbush covers a vast area round the great "mbuga". It is largely composed of short grass glades with islands of *Commiphora* thicket scattered about in it. The hard pan however is not of even composition but broken by groves of *Acacia kirkii*, occasional baobab trees and clumps of *Salvadora persica*. Much of the hard pan fringing the great "mbuga" contains *Acacia rovumae* and *Lannea humilis*.

'The great Usangu "balali" is fringed by groves of *Acacia seyal* var. *fistula* broken by lanes of a gall-acacia resembling *Acacia formicarum*, which lead up into the hard pan country.

'The hard pan elements are almost exactly like those of the south east margin of the Wembere Steppe; on the other hand the territory occupied by *Acacia tortilis* is more extensive than in the Central Province.

'The great Usangu "mbuga" is literally a natural zoo. Impala were very common and tame. At the time of my visit these animals appeared to be most abundant in *Acacia tortilis* country, where they were probably attracted by

the feed of fallen pods. Zebra are exceedingly common in the great "balali" where during the day time they graze far out into the open plains, but at night, to avoid lion, they come into the open mud flats along the edge. During the rains when the plain is flooded these herds of zebra are driven back into the dry *Acacia tortilis* and miombo country on higher ground. A few elephant were present at the time of my visit; they frequented the miombo and hard pan, drinking at night at the very numerous springs which emerge along the margin of the *Brachystegia* hills. However, during the rains very great numbers of elephant come into the villages in the hard pan and reside there for some months during which time much damage is done to native crops. The hard pan areas show an amazing profusion of foot prints of elephant, and the natives state that they are often to be seen during the day time in the open. A few giraffe were seen along the margin of the "balali" but these animals were by no means common at the time of my visit. Wart hog and duiker are to be seen occasionally, and spoor of greater kudu was also observed.'

To this I would add that dikdik and game birds were also very common; that I did in fact meet elephant in the open; and that from the air Burtt and I saw many herds of elephant and some buffalo in the Usangu swamp. Of these flights Burtt writes: 'Flying towards Mbeya we pass low along the margin of the plain and see numerous herds of zebra, eland, giraffe and impala, while out in the open are small groups of dismal looking topi. Distant herds of elephant can be recognised by the white plumage of tick egrets which are sitting on the backs of the animals as they quietly pasture.'

#### 4. ABERCORN, NORTHERN RHODESIA

'Such genera as *Acacia*, *Commiphora*, *Grewia*, *Albizia* and the whole family of Capparidaceae of the thornbush country of Tanganyika Territory are very poorly represented in Northern Rhodesia, because of the dominating *Brachystegia* complex. *Acacia albida* of the Lake bays, *Acacia sieberiana* of the high "dambo" margin and *Acacia holstii* on rocky slopes are the only representatives of the genus. In places, especially near the Lake coast, we find *Commiphora stoltzii* occurring in the limited transition zone between *Brachystegia allenii* and the Lake bays; this plant resembles *Commiphora fischeri* of Tanganyika Territory but has two pairs of leaflets. Such plants as Capparids, *Commiphora pilosa*, *Combretum queinzii* and *Grewia* occur only on termite mounds in the general *Brachystegia* complex. Conversely, genera such as *Uapaca*, *Protea*, *Monotes* and *Cryptosepalum*, which are rare in northern Tanganyika, are well represented in the Abercorn District.'

## IV. DECIDUOUS THICKET

## 1. THE LAKE PROVINCE

(i) *Primaeval hill thickets.*

'The Lake Province hills stand out of the vast alluvial plains of cultivated Usukuma (Phot. 36, 38) and extend northwards in scattered groups of fantastic and isolated granite kopjes or ridges to the shore of Lake Victoria. The Mantine hills, Usanda and the Tinde hills, the Buhungukira hills, the Kimali hills of Maswa District, and the hills of Mwanza are typical.

'The primaeval thicket is composed largely of deciduous trees interspersed with coppicing shrubs and climbing plants some of which (*Strychnos matopensis*, *Teclea nobilis*, *Tricalysia cacondensis* and *Maba abyssinica*) are evergreen. The canopy may vary from 8 to 30 ft. in height, and be pierced in places by rock faces which succour a xerophytic vegetation in cracks and crevices: *Aloe* spp., *Pentas graniticola*, candelabra Euphorbias, *Sansevieria* spp. and *Haemanthus filiflorus*.

'The Usukuma hills (Phot. 35) are characterised by the olive green canopies of *Commiphora eminii* (Phot. 34) and white masses of *Dombeya* blossom in the early rains. In the densest thickets the grass canopy is entirely suppressed, the floor of the thicket being composed of decayed leaves and twigs which form a thick humus. However in glades we find a carpet of grass, *Oplismenus boehmannii*, studded with blue labiates, *Plectranthus flacidus*, and small white "lilies", *Chlorophytum* sp. The explorer of the thicket will have to cut his way through the denser parts with a "panga" and will find the thorny branches of *Acacia pennata* particularly troublesome to his progress, while the tangle of thornless *Acalypha engleri*, *A. fruticosa* and *Justicia salviooides* will offer considerable resistance.

'In the Shinyanga thicketed hills the higher and more open parts are decorated with pale blue and ochre flowers of the shrubs *Barleria splendens* and *Tinnea aethiopica*, and on Usanda we find a coppicing thicket of *Burttia prunoides*. The northern Usukuma and Lake coast hill thickets are rendered obnoxious by the painfully stinging climber *Urera fischeri*, while the decorative "pawpaw" like *Obetia pinnatifida* must be avoided at all costs, together with the large nettle *Girardinia condensata* of the Mantine hills.

'Primaeval hill thickets are easily destroyed by grass fires, and are replaced by grass savannah with fire resistant species, taking the place of the former forest, such as *Combretum gueinzii*, *Erythrina abyssinica*, *Ostryoderris stuhlmannii*, *Acacia holstii*, *Sterculia quinqueloba*, *Commiphora fischeri* and others. The exclusion of grass fires will quickly be followed by secondary thickening, but no doubt a vast period must elapse before a forest simulating the primary one is attained.'

On the kopje at Old Shinyanga, 'the bulk of the north and west sides of the hill have been cleared of thicket by the natives cutting firewood and by the

seasonal grass fires. The cleared grass slopes show up sharply against the clean fire scarred margin of the existing thicket. Among the grasses *Hyparrhenia* sp., *Panicum maximum* and *Sehima nervosum* are the principal species, the first growing to 7 ft. On the west slope of the hill the grass fire has not entered for a season with the result that the many coppicing stumps of shrubs hitherto suppressed are growing up rapidly, conspicuous species being *Acalypha engleri*, *Abrus schimperi*, *Dalbergia ochracea*, *Dombeya quinqueseta*, *Markhamia acuminata* and *Lannea fulva*. The tall *Hyparrhenia* is being suppressed by the coppice whose shade encourages a number of coarser leaved herbs, *Commelina* sp., *Acalypha ciliata*, *Cleome hirta*, *Hibiscus angulatum* (a tall woody herb), *Leonotis nepetifolia*, *Monechma vibracteatum*, *Pycnostachys dawei*, *Sesamum* sp., *Solanum renscii* and various Vernonias including *V. stenolepis*. There is little doubt that after two or three seasons the burnt grassy areas would regenerate to the dense deciduous thicket that clothes the other parts of the hill.'

Of the Shinyanga hills in general, Burtt writes:

'These thickets resemble very greatly the natural deciduous thickets on the decayed granite soils. However, the presence of the trees peculiar to the higher granite hills such as *Combretum molle*, *Ficus sonderi*, *Maba abyssinica*, *Cassipourea mollis*, *Pappea ugandensis*, *Vitex keniensis*, etc. which grow in the age-old leaf litter between the great rocks, indicates a plant succession going beyond that of the thicket alone that is the climax of the lower country.'

'The soil is scanty, filling the cracks and crevices between great granite boulders; it is dark brown, greyish or almost black and of a soft earthy texture, sometimes with white sand grains overlying the soil in a thick layer of leaf litter in various stages of decay.'

#### (ii) Eluvial thickets.

Away from the hills, 'eluvial thickets are to be found scattered about in the *Combretum* woodland of Shinyanga. They are most frequent on the crests of undulating country where there are often outcrops of low rounded granite boulders or the rugged exposure of a murram pavement. The thickets may be over a quarter of a mile wide but are usually smaller.'

'As one approaches the eluvial thicket one sees in the rainy season the tops of baobabs or the spreading canopy of the large tree *Entandrophragma bussei*, and the rounded crowns of *Sclerocarya birrea* var. *multifoliolata*, sticking out of a continuous wall of greenery which is largely composed of *Commiphora ugogensis*; *Commiphora stuhlmannii*, *Strychnos heterodoxa*, *Markhamia acuminata*, *Dombeya* sp. and the wild flamboyant, *Delonix elata*, which bears attractive, sweet scented flowers, yellow and white in colour. Among the trees grow straggling coppice shrubs of *Grewia platyclada*, *Hippocratea loesneriana*, *Dalbergia ochracea* and the tormenting shrub *Acacia pennata*.

'To explore the eluvial thicket a path has to be hacked with a "panga" through the outside fringe of *Abrus schimperi*; but once inside progress is

much easier and we wind our way through and over a mass of tangled branches and see that the thicket floor is covered with leafy humus, out of which grow a multitude of saplings of different trees including baobabs, and the dark green leaves of *Sansevieria*. The more open parts of the thicket are decorated with herbs such as *Hibiscus dongalensis*, *Gladiolus hanningtonii*, *Aneilema johnstonii* and that pretty flowered but obnoxious weed *Hibiscus harstersianus*.

'The surface soil is covered with a layer of leaf litter and twigs which form a humus. The thickets are often clustered over broken blocks of murram or granite and dolerite boulders, but where the soil is deep clearing of the thicket produces good crops.'

'The annual grass fires sweep with great severity up the grass lanes but do not penetrate the thicket to any extent, only singeing its margins, or, where the full force of the fire comes up to the thicket, gradually eating bays into it. In other places on the leeside, the thicket advances invading the savannah, and in the course of many years may have completely altered in outline, having included in its mass various trees that were previously isolated in the savannah.'

## 2. ABERCORN, NORTHERN RHODESIA

### (i) *River gorge thickets.*

Through the vast *Brachystegia* forests southward from the Lake Province to the border of Tanganyika Territory, extensive thickets are lacking. But in the Abercorn District of Northern Rhodesia, 'thickets in the rocky gorges of the Lucheche, Izi, Mwambeshi and Lunzua rivers are of great interest as they contain certain shrubs (or their near relatives) only seen previously in the great Itigi thicket of the Central Province of Tanganyika Territory (see p. 104). The following species were collected: *Baphia massaiensis*, *Burttia prunoides*, *Pseudoprosopis fischeri*, *Craibia* cf. *burtii*, *Indigofera subcorymbosa* and *Haplocoelum foliolosum*. A small *Landolphia* was generally common.' *Combretum celastroides*, related to *C. trothae* of the Itigi thicket, was also collected.

On the shores of Lake Tanganyika in this region, 'shingle beaches are found for the most part at the foot of small cliffs cut back into the *Brachystegia allenii*-covered rocky hillsides, or flanking the fault scarps in which the Lake is cradled. The constant pounding of storms together with the fall of lake level has caused a slope of loose shingle to be formed at the foot of a small cliff 30 to 60 ft. high, and to drop below abruptly into deep water.'

### (ii) *Lake cliff thickets.*

'The cliff and shingle beach are usually clothed with deciduous thicket, composed of coppicing shrubs *Grewia platyclada*, *Baphia massaiensis*, *Bauhinia petersiana*, *Dalbergia nitidula*, *Vitex radula*, *Plumbago zeylanica*, *Bridelia fischeri*, *Ochna* sp., *Rhus villosa*, *Canthium* sp., *Triaspis speciosa*, *Clerodendrum myricoides*, *Cassytha filiformis*, *Phyllanthus* sp., *Mucuna* (buffalo bean), *Abrus*

*praecatorius*, a shrubby *Euphorbia* and *Sterculia africana*. *Commiphora kyimbilensis* is common (Phot. 33). Ten to fifteen feet from the foot of the cliff the following trees appear: *Ficus sycamorus*, *Commiphora puguensis*, *Sterculia quinqueloba*, *Landolphia* sp., *Commiphora pilosa*, *Burttia prunoides* and *Diplorrhynchus mossambicensis*, with scattered *Pterocarpus chrysotricha*, *Brachystegia spicaeformis* and *B. allenii*. At about 30 to 60 ft. the thicket gives place abruptly to open *Brachystegia allenii* woodland which is burnt by grass fires.

'The shingle washed by waves was usually clothed with a fringe of *Phragmites communis* and a tall grass both growing in standing water and forming a belt 4 to 10 ft. wide, which was observed to be much tunnelled by crocodile and hippopotamus—the former climbing on to the shingle to sun themselves in small glades. In some places the fall in lake level had exposed a sill of shingle 6 to 20 ft. wide between the thicket and the *Phragmites*; this sill was invariably clothed with a stand of *Trichopteryx*, a grass 6 to 7 ft. in height and used for thatching huts by the local natives.'

### 3. DOMIRA BAY, NYASALAND

'Deciduous thickets occur in various ravines and on rocky hills, and wherever fires have been excluded from the *Combretum* woodland area. They are composed of *Grewia*, *Allophylus*, *Antidesma venosum*, *Bauhinia petersiana*, *Hippocratea*, *Popowia obovata* and *Dichrostachys*'.

### 4. THE CENTRAL PROVINCE

#### (i) *Primaeval hill thickets*.

Primaeval thicket of the type described under 'the Lake Province' is found on the Central Province hills, which 'are very largely in the nature of escarpment faces protruding from the *Brachystegia*-covered plateau, such as the Rift Wall, and the Iambi and Isansu hills in Mkalama District or the Chinene Hills north of Dodoma; or groups of rocky hills as in Usandawe, Sambala and Dodoma; or isolated hills which include such eminences as Manyoni kopje and Swagaswaga.'

#### (ii) *The Itigi thicket*.

'Primaeval deciduous thicket of the Itigi type is almost entirely peculiar to the Central Province where it is especially developed in the Districts of Manyoni and Singida; outlying areas occur in southern Mkalama, western Kondoa, Dodoma and Mpwapwa Districts and extend over the provincial boundary into north-east Tabora.' The presence of certain elements of these thickets in the Abercorn area has already been noted.

'This remarkable vegetation type (Phot. 40, 42, 43, 45, 46) is composed almost entirely of various species of much branched, coppice forming shrubs,

growing from 8 to 15 ft. in height. The shrubs are evenly spaced, giving on the whole an open appearance when viewed from inside the thicket, while the shrubs themselves are interlaced overhead to form a thick, even a continuous canopy that becomes very dense in leaf flush, and shows amazing uniformity when viewed from an aeroplane. The canopy may be pierced by flat topped trees 25 ft. high of *Albizia brachycalyx*, while it is broken, especially in the remoter parts of the thicket, by evergreen woods of *Craibia burttii* 20 to 35 ft. in height; these woods are readily seen from the air, and on air photographs show up as peculiar grey mottlings amid the even blackness of the general thicket canopy (Phot. 45).

'The eastern Itigi thicket north of Manyoni and along the Rift escarpment towards Singida, and south of Manyoni towards Saranda, Kilimatinde and Iseke is dominated by the shrub *Pseudoprosopis fischeri* (Phot. 44), whose creamy white catkin like flowers appear in profusion about December and permeate the air with their fragrance to excite the admiration of the traveller at the window of his compartment, as the train labours up the steep incline of the Rift escarpment towards Saranda station, and he gazes out over that ever widening sea of thicket that separates him from the receding Kilimatinde plains.

'The western expanse of the great thicket is dominated by the coppicing shrub *Baphia massaiensis* with beech like foliage. (The Rift Wall marks the eastern edge of the continuous thicket block and is clothed with an almost pure thicket of *Baphia burttii* whose branches have an erect habit, differing from its more straggling relative.) Almost universally distributed throughout the thicket is *Bussea massaiensis*, a tree growing sometimes as high as 20 ft. and characterised by its golden-yellow, *Cassia*-like flowers in the spring. The wood of *Bussea* has remarkable qualities of hardness and durability, being completely termite proof; the older trees are hollowed with age and frequently harbour bees whose honey is much sought after by natives. The seeds are about the size and shape of ground nuts and also are regarded by the natives as a delicacy.

'Throughout the thicket we find the coppicing shrubs *Combretum trothae*, *Grewia burttii* and *Tapiphyllum floribundum*, while, towards the centre of the great thicket, we may find that a certain evergreen element has crept in, which is denser than the thicket as a whole and is composed of the privet like shrub *Tricalysia cacondensis*, the low shrub *Teclea fischeri*, and *Rothmannia fischeri*, a tree with large and highly scented, trumpet like flowers. In these partially evergreen areas there are almost always an abundance of single stemmed small trees such as *Canthium burttii*, *C. huillense*, *Haplocoelum foliolosum*, *Ochna* sp. and *Cassipourea mollis*, whose white lacy flowers smell exactly like cucumber salad. Lastly we have the remarkable shrub *Burttia pruinoides* (Phot. 41) with cherry blossom flowers and gaily coloured rosettes of young foliage appearing with the first rains about December.

'The Kazikazi [western] thickets are composed of the same species of plants as the Manyoni-Kilimatinde end of the great thicket area, except that the coppicing shrub *Pseudoprosopis fischeri*, which is almost dominant in the eastern areas, does not appear in the western region of the thickets. The occurrence of so many novelties among the relatively few components of the thicket and the conformity of the thickets themselves to the peculiar cement soils suggest that the thickets are of vast age and definitely not the result of human interference to a previous vegetation type.'

'These deciduous thicket areas are divisible into two distinct floristic types, open deciduous and dense deciduous with evergreen elements:

'Open deciduous thicket is composed of coppicing shrubs with interlacing canopy 15 to 20 ft. in height; found on the lower and sloping portions of the thicket plateau on greyish-yellow soils of a soft and loamy character. The open thicket is dominated by *Craibia burttii*, *Baphia massaiensis* and *Combretum trothae*, with *Grewia burttii*, *Burttia prunoides* and *Bussea massaiensis* very frequent. The smaller shade-bearing shrubs *Justicia salvioides*, *Croton polytrichus* and *Indigofera subcorymbosa* are fairly frequent, but not in sufficient quantity to impede progress through the thicket, as the spaces between the shrubs are sufficiently open to allow a man to pass without undue stooping, while such animals as greater kudu pass freely.'

Dense deciduous thicket with evergreen elements 'is found on the crests of the plateau on very hard, cement-like, light whitish-grey soils. It is composed of closely-growing, many-stemmed shrubs with relatively open canopy 12 to 15 ft. in height, and is dominated by *Cassipourea mollis*, *Tapiphyllum floribundum* and *Bussea massaiensis*, with *Craibia burttii*, *Tricalysia cacondensis*, *Combretum trothae*, *Grewia burttii* and *Baphia massaiensis* occurring commonly, while the spaces between the shrubs are closely filled with saplings and thick scrubby plants like *Justicia salvioides*, *Croton polytrichus*, *Indigofera subcorymbosa* and *Teclea fischeri*. So dense is this thicket that man can only pass through with the greatest difficulty, while greater kudu, from observations at Kazikazi, do not appear to enter it at all. Elephants in their wanderings pass through the dense thicket but do not form regular paths, as the shrubs spring back behind them.'

'Along the Kazikazi-Mihama path where it had been widened to admit the passage of motor-cars through the Beruda thicket, certain plants alien to the thicket community appeared, namely *Bidens hildebrandtii*, *Leonotis nepetifolia*, *Leucas neuflesiana*, *Vernonia poskeana* and the slender grass *Anthephora burttii*'.

'A small *Usnea*-like lichen appears frequently in the thicket on *Tapiphyllum* shrubs, while a silvery-grey encrusting lichen is very common on the older wood of the smooth-barked coppicing shrubs *Combretum trothae*, *Baphia massaiensis* and *Bussea massaiensis*.

'It is of interest to note that the shrub *Burttia* has a finely reticulate,

lightish brown bark; *Tricalysia* has a flaking striated bark of brownish-grey colour; *Indigofera subcorymbosa* has a dark grey-brown bark heavily spotted with light brown lenticels; *Justicia salviooides* possesses a characteristic bark of dark green; and *Croton polytrichus* has pubescent light brown patches. With these exceptions the dry season aspect of the thicket coppice is uniform silvery-grey.

The soils vary in depth from 2 to over 10 ft. and are of a sandy nature, and almost uniform in colour except for a few inches at the surface which is brown with leaf debris. The soil is soft in the rainy season but hardens considerably on drying. It overlies a peculiar rock formation termed "duricrust" or "cement" which overlies in turn the granite floor. Near Saranda the thicket soils are bright terracotta red, while at Itigi and Kazikazi they are either buff or ashy grey in colour. In some areas a reddish-purple sand is washed out of the thicket soils and lies on the road surface or paths. The soils absorb moisture readily and show little sign of surface erosion except locally near the Rift escarpment. Analysis of the Kazikazi soils by the Soil Chemist at Amani has shown them to be of high acidity.

Elephant are resident during the dry season, feeding on the seeds of *Grewia burttii* and *Grewia platyclada*. At night time they come out of the thicket to tear off branches from the *Isoberlinia* and *Brachystegia* trees in order to indulge in their favourite pastime of chewing the young bark.

The great thicket when leafless (Phot. 42, 43) assumes a much more open appearance, with the leaf litter carpeting the floor like beech mast; but in full leaf (Phot. 40) the canopy is so dense as almost to exclude herbage with the exception of a slender grass, *Panicum heterostachium*, and various herbs which manage to survive in a dwarfed state such as *Hibiscus harstesianus*, *Bidens lineariloba*, *Tragia* sp. and *Plectranthus*.

During the leaf-fall a considerable amount of leaf litter is produced, that lies entire on the surface of the ground during the dry season. With the advent of the rains most of the leaf litter appears to be removed by the activity of vast armies of small termites, which construct intensely hard, low, grey coloured mounds six inches to a foot in height, working into the reticulate surface quantities of reddish sand grains that give these termite heaps a very peculiar and decorative appearance. The termites themselves are small, membranous and fragile looking, measuring about a quarter of an inch in length. Elephant and wart-hog dung dropped in the dry season has been observed to be completely encrusted with their earthy tunnels, and to have all the soft vegetable matter removed leaving only the seeds of *Grewia*.

The large mounds of *Eutermes* (?) with characteristic ventilation shafts are less frequent but evenly scattered through the thickets. The large candelabra Euphorbia, *E. bilocularis*, often grows on these mounds, together with other species alien to the thicket community such as *Cassia singueana*, *Commiphora schimperi*, *C. stuhlmannii* and a herb, *Justicia* sp. near *betonicoides*.

'A peculiar termite nest composed of minute particles of dark brown vegetable matter strongly cemented together by a secretion of the termites into a brittle, scaly, cardboard-like substance, is frequently seen supported in the forks of *Bussea massaiensis* shrubs. These nests are from one to two-and-a-half feet in length and a foot-and-a-half in width, and are connected to the ground by tunnel galleries. The termites themselves are very small and delicate, resembling the smaller species already referred to.'

'It will be seen from the above observations that termites are particularly numerous in the thickets, in which they are definitely responsible for the removal of dead branches from the thicket coppice; the branches are often covered with their earthy galleries.'

'The sharp transition from the thicket to the *Isoberlinia-Brachystegia* or transition woodling is one of its greatest peculiarities. There is no overlap or invasion of one community by the other; often a bare sandy lane to ten yards in width separates the thicket from the community adjacent to it (Phot. 39). It is noted that *Brachystegia* trees fringing the thicket are often stunted.'

'There is considerable traffic of elephant and giraffe and occasional rhinoceros round the thicket margin. These animals in places break up the otherwise continuous margin by untidy pathways that only extend into the thicket for approximately a hundred yards.'

'There is always a gentle slope from the thicket margin down to the bush adjacent to it.'

'The great reproductive capacity of the thicket elements, especially of *Baphia massaiensis*, *Burttia prunoides*, *Combretum trothae* and *Grewia burttii*, is very striking, the Leguminous species littering the ground with their seed in the month of September, while birds and fruit-eating mammals like the civet-cat and elephant are continually dispersing vast quantities of *Grewia burttii* seed. It is remarkable that with the exception of scattered plants like *Burttia* in the *Commiphora ugogensis* and *Isoberlinia-Brachystegia* woods fringing the thickets there is no appearance of seedlings or young plants of the thicket elements in the communities outside the thicket; especially as the *C. ugogensis* and *Isoberlinia-Brachystegia* woods in the neighbourhood of Kazikazi are of peculiar dry type with such scanty herbaceous canopy as to be untouched by the annual grass fires.'

'Although fierce grass fires burn through the transition woodling adjacent to the thickets, the fires themselves do not enter the thicket or burn off the cover of dry leaf litter. An experimental fire was lit in the great Beruda thicket on the 27th October during the heat of mid-day and, fanned by a strong gust of wind, developed into an intensely hot forest fire that incinerated approximately fifty square-yards of thicket, but died out with the fall of the wind. There is certain evidence that the thicket elements when subject to a fierce fire are completely killed, though an incomplete fire allows regeneration to take place from the old root stocks.'

(iii) *The thickets of the Mpwapwa area.*

Farther east, in Mpwapwa District, several types of deciduous thicket are distinguishable.

(a) *Thickets related to the Itigi type.* ‘Deciduous thickets are seen fringing the lower margin of the *Brachystegia microphylla* on hillsides; they resemble, to a certain extent, the semi-evergreen parts of the Itigi thickets, and several species characteristic of the latter are seen commonly: *Cassipourea mollis*, *Indigofera subcorymbosa*, *Justicia salvioides*, *Ochna stuhlmannii* and *Tricalysia cacondensis*. The thicket grasses *Anthephora burttii* and *Gilgiochloa indurata* are common along pathways traversing the thickets. It is interesting to see large spreading trees of *Commiphora ugogensis* in the transition of the Tubugwe thicket with the *Brachystegia* forest, the only locality where this species was observed near Mpwapwa. With the exception of a small leaved shrub, *Vitex* sp., *Hymenocardia mollis* and *Hymenodictyon floribundum*, a medium sized shrub, all the plants recognised in the Mpwapwa deciduous thickets occur in the northern and western parts of the Central Province.’

(b) *Dry ravine thickets.* ‘Dry ravines are common on the lower slopes of the steep hillsides where they traverse the *Isoberlinia-Brachystegia* woodland and deciduous thickets and in many places cut steepsided channels through the eluvial soils. They are choked with dense impenetrable thicket vegetation whose canopy is pierced here and there by larger trees such as *Acacia usambarensis*, *Albizia brachycalyx* or large *Commiphoras*, as *C. zimmermannii*. Smaller trees that feature in the composition of the dry ravines are *Delonix elata*, *Commiphora subsessilifolia*, *C. stuhlmannii* and *Fagara merkeri*, while the most noticeable thicket producing, semi-scandent shrubs are *Acacia pennata*, *Dalbergia fischeri*, *D. ochracea* and *Harrisonia abyssinica*. Less shrubby places are choked with *Disperma crenata* and near Mpwapwa a scandent *Combretum*, *C. padoides*, is seen.

‘The dry ravines at Tubugwe contain frequent large, blue-green barked trees of *Commiphora caerulea* with *Indigofera subcorymbosa* as a coppice; while the larger and deeper ravines towards Iringa creek are filled with open woodings of *Combretum schumannii* with shallow-fluted trunks. (This Combretum is common in seasonal water courses along the foot of the Saranda escarpment in Manyoni District.)’

(c) *The Commiphora-Cordyla thicket.* ‘The dry *Commiphora-Cordyla* thicket is not seen in the western and northern parts of the Central Province; it clothes a large proportion of the lower Gulwe-Kimagai valley slopes and the rocky island hills jutting out from them. The dry thickets are largely composed of loosely crowned *Commiphora* trees (mainly *C. hornbyi* and *C. merkeri*) forming an irregular thin canopy above an almost impenetrable scrub of *Disperma crenata*, *Acalypha engleri*, *Croton dichogamus*, etc., that is thickened up in many places by the thorny pink flowered shrub *Caesalpinia trothae*, and

by *Acacia pennata*, *Hippocratea loesneriana*, *Grewias* and many other woody scandent plants. Standing out of the general canopy are large trees of *Entandrophragma bussei* and the tall, paper-barked *Albizia tanganyicensis*; and baobabs are frequently seen. *Cordyla africana* with its *Cassia*-like leaves together with *Acacia kiniunge* (Phot. 25) are features of the dry thicket. (This *Acacia* occurs also along the Rift scarp near Kilimatinde.) *Grewia villosa*, *G. dumicola* and *Cordia* sp. were also observed.

'In the higher levels of the thicket the following plants were noted: *Albizia harveyi*, *Bauhinia fassoglossensis*, *Croton sheffleri*, *Euphorbia espinosa*, *Ehretia tetrandra*, *Helinus ovatus*, *Hippocratea buchananii*, *Indigofera subcorymbosa*, *Lannea stuhlmannii*, *Strychnos heterodoxa* and *Jasminum parvifolium*.

'The dry thickets extend about half way along the railway towards Dodoma, where a sudden transition to granite soils (according to Mr C. Gillman) is accompanied by a correspondingly sharp change from the *Commiphora-Cordyla* type of thicket to deciduous thicket of the Itigi type.

'In the more xerophytic areas of the dry thicket we find *Salvadora persica* (the native's toothbrush), *Sarcostemma viminale* and *Fockea schinzii*, the last with a peculiar snake-like climbing stem and milky latex.'

Of the plants composing this dry thicket, Burtt notes that only five species, *Caesalpinia trothae*, *Commiphora hornbyi*, *Dirichletia pubescens*, *Cordyla africana* and *Maerua flagellaris*, had not been previously observed by him in the northern and western parts of the Central Province. The altitude of the dry thicket is from 2500 to 3000 ft.

## 5. THE LUKOSI VALLEY AREA, USAGARA

### (i) *The Commiphora-Cordyla thicket.*

'As soon as we have left the pleasant country at the top of the Katonga pass [going from Iringa towards Kilosa] we descend about 2000 ft. to what at this time of the year [October] is leafless *Commiphora* desert thorn country to the south. This vast desert area appears at first flat but is in reality undulating country traversed by dry water courses in quartzite debris. To the east it is flanked by the steep Imagi and Kikima mountains which are the eastern outliers of the Iringa highlands; the Imagi mountain is capped by evergreen forest while its slopes at the time of my visit showed the roseate flush of *Brachystegia* woodland. On the north east bank of the Ruaha are the steep sided mountains of Mbaga and Mgongwe largely clad with *Commiphora* thicket, and in the centre and dominating the whole area is the castellated peak of Kombaguru.'

'Through this vast *Commiphora* desert the Lukosi river has carved its way to the Ruaha—a raging river plunging over a boulder strewn bed often restricted to gorge like narrowness. Its course is marked out by the green

contrast of its evergreen trees with the silvery-grey desolation of the leafless *Commiphora*. At the confluence of the Lukosi with the Ruaha we look with disappointment at a vast furrow amid mud banks where the river winds its serpentine way from the desert to the north to lose itself in a mountain-locked trough to the south east, giving one the impression that the great river is flowing in the wrong direction!

'The *Commiphora* desert thicket is the exact counterpart of that in the Gombo-Kidete valley, dominated by the scaly barked *Commiphora merkeri* and the bleached, green-yellow skeleton trees of *Commiphora caerulea* and *C. hornbyi*, with *Cordyla africana*, *Acacia keniensis*, *Commiphora stuhlmannii*, *C. sarandensis* and *C. schimperi* (?). Here and there are large *Entandrophragma bussei* and baobab trees, while a medium sized *Sterculia* allied to *S. africana* is common. On rocky places grow scattered candelabra Euphorbias (*E. nyikae* and *E. bilocularis*) with *Delonix elata* and *Grewia dumicola*. The spiny and amazing tree *Sesamothamnus busseanus* is frequent. Grass growth is scanty in the extreme and is mostly replaced by scrub of "fireweed", *Barleria* sp.

#### (ii) *The Salvadora* thicket interzone.

'The *Salvadora* thicket interzone [between the *Commiphora* thicket and the riverine forest of the Lukosi river] extends down the river to the Ruaha; it is from 10 to 100 yards wide and almost impenetrable. Out of the *Salvadora* grow candelabra trees, *Euphorbia bilocularis*, while glades contain *Commiphora subsessilifolia*, *Ximenia americana* and *Delonix elata*. This area is grassless but is in places cultivated. It resembles the country near Kimagai Lake at Mpwapwa.'

### V. COMBRETUM COMMUNITIES

Though Combretums are scattered through almost every other vegetation type, they often form, sometimes with *Terminalia* or *Acacia* spp. (Phot. 48), separate communities either covering large areas, like the *Combretum ghasalense* on ironstone hills of the Lake Province, or narrower interzones between more extensive woodlands of other kinds.

#### 1. THE LAKE PROVINCE

##### (i) *Combretum-Ostryoderris* communities.

'The *Combretum Zeyheri-Ostryoderris-Terminalia sericea* woodland is a feature of the Shinyanga woodland types (Phot. 47), and is found on higher ground or between the *Brachystegia spicaeformis* woodland and the hard-pan alluvium below. It is found to a lesser extent in Maswa District, but its distribution has as yet been little worked out. There is little doubt that much of the cultivation steppe of Usukuma was formerly clothed with this type.'

'The *Combretum* woodland of Shinyanga is composed of trees of *Combretum*

*zeyheri* and *Ostryoderris stuhlmannii*. Everywhere are large scattered trees of *Commiphora ugogensis* under which one will often see scrub of *Abrus schimperi*. Large solitary baobabs are a feature of the landscape, while in places are dark impenetrable masses of thicket.

'The tree species composing the Shinyanga woodland are very much the same as in the Central Province (see p. 114) except for bushes of *Heeria reticulata* on the higher ground and in some areas the large grey pillar trunks of *Berchemia discolor*. *Acacia benthamii* is also very frequent. The grasses are poorer in species, being usually pure stands of *Hyparrhenia rufa* growing 5 to 6 ft. in height, or in places large areas of *Panicum maximum*. Together they form a thick mass difficult to walk through and saturated with dew in the early mornings [at the colder times of year]. However, in the dry season the grass fires are severe.'

In the Shinyanga and Maswa districts *Commiphora fischeri*, replacing *Combretum zeyheri* may, co-dominate with *Ostryoderris*. These Commiphoras, so much resembling apple trees, may with the larger *Ostryoderris* form remarkably pure stands over large well-grassed areas on eluvial soil, and form the true 'Orchard bush' or 'Obstgartensteppe' as originally described by Hans Meyer (1892), though these terms have subsequently been more loosely applied to various *Combretum-Commiphora* associations.

'The exclusion of fires results in three or four years in the production of an impenetrable thicket, largely composed of *Combretum* suckers and *Dichrostachys glomerata*, which kill all the grasses and are no doubt the foundation of the eluvial thicket, which in years gone by must have covered the whole of this vegetational area.'

'Giraffe are commonly seen in this *Combretum* woodland, with eland and occasional roan. Herds of impala may also be seen.'

'The soil is reddish-brown in colour when dry, and brownish when wet; it sets hard in the dry season but with the rains becomes easy to cultivate. The subsoil is full of decayed granite fragments, known as "changalawe", at about 2 to 6 ft. There may be either a murram pavement of iron deposited by solution, or the granite bedrock. The soil is of acid character.'

#### (ii) *Combretum-Afrormosia* communities.

In western Mwanza District near Lake Victoria, 'fringing the valleys is a belt, from 100 to 300 yards wide, dominated by *Afrormosia angolensis* trees of unusual size in eastern Karumo, smaller as one proceeds westwards. Associated with the *Afrormosia* are trees of *Combretum grandifolium*, some of great size, *Combretum ghasalense* and an unknown *Terminalia* with large and dark green foliage.'

'The grass canopy is usually a pure stand of *Trichopteryx* sometimes interspersed with *Hyparrhenia*.' Patches of woodland dominated by *Afrormosia* also occur in the Nindo area of western Shinyanga.



Phot. 39. The open sandy strip between the miombo (*Brachystegia spiciformis*) woodland and the wall of the Itigi thicket on the right. Near Kazikazi; dry season aspect (pp. 84, 108).



Phot. 40. Itigi thicket pierced by the Central Railway. Wet season (pp. 104, 107).





Phot. 41. *Burttia prunoides* in young leaf in the Itigi thicket (p. 105).



Phot. 42. A game path through a mile-wide 'neck' of the Itigi thicket; dry season aspect. For wet season aspect of thicket see Swynnerton (1936), Plate 17, fig. 2 (pp. 104, 107).





Phot. 43. An elephant path to an open 'island' in the Itigi thicket; dry season aspect. This path is seen from the air in Phot. 45 (pp. 104, 107).



Phot. 44. *Pseudoprosopis fischeri* in fruit. This plant is in the open, but the species dominates much of the densest Itigi thicket near Manyoni (p. 105).





Phot. 45. Aerial vertical photograph of the Itigi thicket. Dry season aspect. The darker mottlings are termite mounds; active ones with white tops are seen on the left near the top of the picture. Pale mottlings on the right are groves of evergreen *Craibia burttii*. In the left-hand bottom corner is miombo woodland, from which an elephant path is seen entering the thicket in the left-hand top corner (pp. 104, 125).



Phot. 46. Aerial oblique photograph of the Itigi thicket. Dry season aspect. In the foreground the hard pan thickets occupy paler areas intersected by darker drainage lines. In the middle distance *Combretum* savannah occupies generally paler soil. In the background is a great block of thicket (pp. 104, 114).





Phot. 47. *Combretum zeyheri* savannah in Shinyanga, in the early rains with grass still short. The plant in the extreme foreground is *Markhamia obtusifolia*, and a *Combretum zeyheri* is just behind it (p. 111).



Phot. 48. *Combretum* savannah near Morogoro, with *Acacia nigrescens* (co-dominant) in centre; here the grass is higher, though not yet fully grown (p. 111).



## 2. TABORA

## (i) Combretum-Afrormosia communities.

A similar vegetation type to that just described characterizes the extensive flood plains of the Igombe and Ugala rivers, and is found in smaller patches elsewhere.

The grassy flats are studded with large termite mounds carrying thicket and tall trees. Between the mounds the dominant large trees are *Afrormosia angolensis*, *Pterocarpus chrysotricha* and *Terminalia torulosa*, while locally there are extensive savannahs of the tall palms *Borassus aethiopum*. Large *Vitex cuneata*, *Terminalia sericea* and *Combretum grandifolium* are scattered widely, and there is a great abundance of the small trees *Combretum ghasalense*, *Combretum* sp., *Crossopteryx febrifuga*, *Mundulea sericea* and *Gymnosporia nemorosa*. *Combretum zeyheri* may be common also, and here and there are stands of *Acacia macrothysa* and the superficially similar *Entada abyssinica*.

The dominant grass is *Laudetia (Trichopteryx) simplex*, and the characteristic antelopes are topi and oribi, though many others occur.

The soil is clay covered with a thin sandy wash.

## (ii) Combretum-ghasalense communities.

Throughout Kahama and Tabora Districts of the Western Province, in the clay-bottomed valleys descending between hill spurs or sprawling indiscriminately between the miombo of the flatter lands, *Acacia* communities are relatively restricted in area and are largely replaced by pure stands of *Combretum ternifolium*, with occasional larger trees of *Terminalia torulosa* and *Combretum grandifolium*, the latter more especially near the line of contact with the miombo.

The grass growth is uniformly long, and usually burnt completely by the annual grass fires. *Hyparrhenia*, *Laudetia simplex* and locally *Schizachyrium schweinfuerthii* are the dominant grasses.

## 3. THE BUA RIVER, NYASALAND

*Combretum ghasalense* communities. 'This [Combretum] country occupies the territory between the Bua and Mudi rivers; it also extends as a wedge between the Bua and the Nambuma. To the east and south it extends over a wide piece of country towards Lilongwe and Mponela on the great north road. The soils are iron-red and of a loamy clay texture and support very tall grass which grows 8 to 10 ft. high. The trees are more widely spaced than the trees in the miombo. Trees of *C. ghasalense*, *Combretum zeyheri*, *C. gueinzii* and *C. cf. binderanum* are distributed throughout the woodland and are of medium height. *Acacia campylacantha* dominates in some of the *Combretum* woodland near the rivers and on certain flat areas of country.'

'*Parinari curatellaefolia*, *Bauhinia thonningii*, *Thespesia garckeana*, *Diplorrhynchus mossambicensis*, *Strychnos heterodoxa*, *Ziziphus* sp. and *Afrormosia angolensis* are common everywhere, and there are some *Dichrostachys* thickets. In some areas the tree *Pterocarpus rotundifolius* is locally common.'

#### 4. DOMIRA BAY, NYASALAND

##### (i) Combretum-Ostryoderris communities.

'The *Combretum zeyheri-Ostryoderris-Terminalia sericea* woodland very much resembles similar woodland near Morogoro in the Eastern Province of Tanganyika Territory. It is dominated by the above-mentioned trees but mixed with many others such as *Albizia harveyi*, *A. amara*, *Acacia benthamii*, baobabs (*Adansonia digitata*), *Afrormosia angolensis*, *Bauhinia petersiana*, *Cassia abbreviata*, *Combretum fischeri* and *Crosopteryx febrifuga*, with occasional *Acacia nigrescens* and *A. goetzei*. The soil is a rich brown loam carrying a fair grass cover, 4 to 6 ft. high, of *Hyparrhenia* spp. and *Panicum maximum*.

'It was seen that fire exclusion here rapidly produced a densification of thicket.'

##### (ii) Combretum ghasalense communities.

'The *Combretum ghasalense* woodland clothes the seasonally wet, low-lying, brown clayey soils. It is composed of very pure stands of *Combretum ghasalense* trees 10 to 15 ft. high, interspersed with *Bauhinia thonningii*. The grass growth is very tall, 6 to 8 ft.'

#### 5. THE CENTRAL PROVINCE

'The *Combretum zeyheri-Ostryoderris stuhlmannii-Terminalia sericea* woodland is found fringing much of the great Itigi thicket, occurring between the thicket and the hard-pan of the valleys. It is also common along the margin of the Wembere Steppe and is found along the foot of the Bereku Ridge.

'If we have been following a path or road gradually descending through Itigi thicket or miombo woodland, we may quite suddenly come out into a very much more open woodland dominated by *Combretum zeyheri*, *Terminalia sericea* and the ash like tree *Ostryoderris stuhlmannii*. If we look back we shall see the unbroken wall of the thicket margin or the edge of the *Brachystegia* wood, cut off from this new vegetation type as if by man's ingenuity—there is no invasion or attempt at colonisation of the more open country either by the miombo or by the thicket; and, from the air, the boundary between the two types is as well defined as the colour patterns on a carpet, a state of affairs which in all probability is brought about by a soil difference, suggested by the grass canopy which is rich in species and differs from that found in either the hard-pan or the miombo (Phot. 46).

'The *Combretum* woodland is not the home of Acacias, but we shall see quite commonly flat topped trees of *Albizia harveyi* which in the distance look

like them. The dark and finely reticulate trunks of *Combretum gueinzii* are seen everywhere; also *Commiphora fischeri*, *C. pilosa*, *Lannea schimperi*, *Lonchocarpus eriocalyx*, *Strychnos heterodoxa* with its smooth grey, beech like bark, and *Markhamia obtusifolia*. In the dry season the large four winged fruits of *Combretum zeyheri* cannot fail to be noticed, especially when a gust of wind scatters them over the ground before us. The small wooden pear-shaped fruits, split in half, of *Schrebera kiloneura*, and the large green cricket ball fruits of *Strychnos innocua* and *Strychnos spinosa*, are also a feature of this woodland. Large *Brachystegia*-like trees of *Afzelia quanzensis* are seen occasionally, and with the early rains the attractive pink and scented flowers of *Strophanthus eminii* appear. Just before the rains the air becomes permeated with the scent of flowers, the sweet lilac scent coming from the golden blossoms of *Cassia abbreviata*, and the unpleasant, nauseating urine odour from *Dalbergia stuhlmannii*.

'As we pass through the *Combretum* woodland we see that the ground slopes gradually down towards the valley; we may catch glimpses of the hardpan country. Large termite mounds feature everywhere, often supporting a solitary large candelabra *Euphorbia* or baobab, *Commiphora stuhlmannii*, dark green shrubs of *Boscia pachysandra* and *Cassia singueana*.

'The *Combretum* woodland as already mentioned is well grassed. The first species to appear are the golden foxtail *Setaria aurea*, *Eragrostis* spp., *Sehima nervosum*, and *Panicum maximum* under the larger trees. In the long rains swathes of *Hyparrhenia rufa* appear which crush out the earlier grasses. All along the thicket edge we find the amazing giant oat-like grass, *Trichopteryx superba*, with flower heads borne on long yellow, leafless stalks 6 to 7 ft. in height.

'Game spoors are common and giraffe are often seen standing about under the trees in the mid-day sun, while in the evening wart-hog root up the soil before retiring into the thicket to sleep. Along the edge of the thicket there is often a well worn sandy elephant path on which we may see the spoor of roan and greater kudu. Dikdik are common, coming out of the thicket to feed at night, while in the dry season we may see the pugs of lion and the three toed print of rhinoceros.

'The grass fires are fierce and keep down all the suckering growth of *Combretum*, *Terminalia* and *Dichrostachys glomerata*—there can be little doubt that fire exclusion would in a few years result in a densification of the bush. But it is doubtful whether the *Combretum* woodland would ever become dense thicket', for this process has not occurred in the *Combretum* woodland of the 'thicket-locked Lambo ya Ngumu north of Kazikazi where fires have never been known to occur. The wooding retains its open character but its components grow crushed together forming stunted entities; the grass growth although of normal composition is scanty because of denser canopy.'

'The soil is of a deeper colour than that of the miombo and more compact,

with less of that loose sandy texture; in the rains it is well drained and easy to cultivate, a fact which accounts for the abundance of native fields and crops on the *Combretum* soil.'

In the eastern part of the Central Province, 'the *Combretum* transition is not very well defined at Mpwapwa; it is found along the lower margin of the *Isoberlinia-Brachystegia* forest, between it and the deciduous thicket. The *Combretum* transition is not so well grassed as the miombo, containing much herbaceous scrub of *Hoslundia opposita* and *Lippia asperifolia*. The following species are common in the *Combretum* transition: *Acacia benthamii*, *Combretum fischeri*, *C. queinzii*, *C. zeyheri*, *Albizia harveyi*, *Commiphora fischeri*, *C. pilosa*, *Dichrostachys glomerata*, *Grewia platyclada*, *Lannea stuhlmannii*, *Ostryoderris stuhlmannii*, *Steganotaenia araliacea*, *Sclerocarya birrea*, *Strychnos heterodoxa* and *Vitex monbassae*'.

#### VI. PROTEA-DOMBEYA HIGHLAND GRASSLAND

This vegetation type (Plots. 12, 15) is found wherever subtropical evergreen forest at high elevations has given place to grassland, probably through the action of fire. It is to be found in all such situations in the Northern and Central Provinces—'the mountainous regions north of Mbulu, the Kiru hills between Ufiume mountain and the Rift Wall, the slopes of Hanang and Ufiume mountains, the higher parts of the Berekü ridge north of Kondoa Irangi, the higher slopes of the Kiboriani hills at Mpwapwa'—and in the Southern Highlands Province in Iringa, Mbeya and Tukuyu Districts.

'The traveller ascends through the cedar like forest of *Brachystegia microphylla* clothing fairly steep hillsides, and at about 5500 ft. leaves this forest more or less abruptly behind him to emerge into fairly open grassland with scattered trees and shrubs hitherto quite unfamiliar to him. The silvery green leaves of "sugar bush" or *Protea* (*P. chionantha*, *P. abyssinica* and *P. uhehensis*) with their enormous heads of creamy-white flowers will be seen scattered commonly about the rich pasture. On the Mpwapwa hills, the Usagara mountains and in the Southern Highlands, he will see commonly the tree *Uapaca kirkiana* with its large, leathery, laurel-like foliage tending to be massed in terminal whorls, and in season bearing abundant fruit resembling and tasting like loquats. Here and there will be seen large flat-topped Acacias, *A. sieberiana* and *A. abyssinica*, the former on the slopes of Ngorongoro forming quite a woodland of well shaped trees. Rocky eminences may be clothed with the bay scented evergreen shrub *Myrica kilmandscharica*, and above Mpwapwa we see everywhere the cypress like shrubs of *Herminiera burttii* endemic in that region.

'In December he will marvel at the flaming red of *Erythrina abyssinica*, a common feature of the highland pasture, and in March and April the whole countryside is decorated with the "may blossom" of *Dombeya quinqueseta*.

Here and there are seen the *Euphorbia*-like trunks of *Cussonia arborea*, large specimens of *Combretum queinzii* and the willow like foliage of *Faurea speciosa*.

'In the spring the hillside becomes a blaze of unusual flowers, blue, white and red predominating, with the yellow hyacinth-like ground orchid *Lissochilus arenarius*, and *Brachycorythis stoltzii*. Perhaps the most beautiful of all are the four-petalled flowers of *Clematopsis oliveriana* which mostly hang their heads of satin whiteness. Later in the season the wealth of flowers is swallowed up by tall grasses (*Hyparrhenia rufa*) and banks of bracken fern (*Pteridium aquilinum*), while the pungent odour of *Helinus* spp. will be noticed as the traveller forces his way across ravines, endeavouring to avoid contact with the dreaded pods of "buffalo bean", *Mucuna foggei*.

'He will find the freshness of the highland pasture restful after the lowland heat; superb views are everywhere at hand. If he chooses to ascend to higher elevations he will come to the subtropical evergreen forest with its sombre greens, capping the hilltops in small forest remnants.

'Fierce fires rage through the highland pasture, in the Northern Province often started by Masai herdsmen to bring on the young grazing. Sometimes large areas escape fires for one or two seasons, in which case the grass growth becomes a matted tangle excluding the galaxy of spring flowers.

'The highland pasture is favoured by zebra, roan, eland, hartebeest and the mountain reedbuck, and is a favourite resort of buffalo and rhinoceros which lie up in the mountain forest during the day-time.

'*Protea-Dombeya* highland grassland is found on red soils of loamy nature which may be of considerable depth; in places they may have been almost entirely washed away, leaving a "skeleton soil" among quartzite pebbles.'

Writing of this type of country at Mpwapwa, Burtt says:

'This type of well grassed open woodland clothes the heavily eroded soils that are in places reduced to coarse gravels (Phot. 12). It is invaded by stunted and wind blown *Brachystegias* (*B. spicaeformis*). On the heavily eroded soils the grass growth is relatively poor, tufts of *Laudetia simplex* being conspicuous. The poor soils support much scrub of *Eriosema ellipticum* and *Smithia speciosa*.

'On richer soils the tall grasses *Hyparrhenia cymbalaria*, *Panicum maximum* and *Pennisetum unisetum* codominate, while bracken and the tall herbs *Leonotis mollissima* and *Pseudarthria hookeri* are common. A large scandent *Mucuna* with robust creamy-yellow inflorescence is frequent in the forest margin together with the aromatic grasses *Melinis* spp.

'Along the western face of the Kiborani range a ridge of quartzite crags traverses the upland savannahs, where huge rocks afford a certain amount of shelter from the grass fires. In such places we find the ornamental shrub *Dissotis melleri* which in December is decorated with spectacular crimson flowers. On the rocks themselves we see quantities of the peculiar *Pandanus*-like shrub *Vellozia*. Both these plants are common also on the upper reaches of Lupanga peak near Morogoro.

'In one sheltered gulley an aged and fire scarred shrub of *Philippia benguelensis* was seen, a survivor of a one time greater Ericaceous thicket that probably fringed the subtropical evergreen forests.'

## VII. EVERGREEN FOREST AND RIVERINE COMMUNITIES

### 1. WEST MWANZA

'Around Geita and the neighbouring hills are lines of tropical forest occupying erosion ravines 50 to 100 ft. deep, carved out of solid sheets of murram (Phot. 52). The forests are composed of the giant trees *Albizia zygia*, *Chlorophora excelsa*, *Cordia abyssinica*, *Mimusops* sp., *Chrysophyllum* sp., *Combretum schumannii* (?), *Rauwolfa natalensis* (?) and giant fig trees.'

### 2. SHINYANGA

'Riverine forest fringing seasonal streams is a common form of woodland, especially along the larger rivers flowing into the Wembere Steppe and Lake Victoria. The Simiyu, the Ninghwa and the Manyonga are typical. The absence of high mountains together with a severe climate causes the principal rivers to dry up completely in the dry season, except for occasional pools along a dry sandy watercourse often hidden by large trees fringing the course of the river. Unlike the forests of the permanent rivers, which are evergreen, the forest of the seasonal streams is deciduous except for large trees of *Ficus sycomorus*, and *Tamarindus indica* which loses its leaves only for a short period.

'The riverine forest of the seasonal rivers also contains large baobab trees (*Adansonia digitata*), *Pipiaadenia hildebrandtii*, *Mimusops densiflora*, *Albizia amara*, *Albizia brachycalyx*, *Acacia campylacantha* and *Kigelia aethiopica* the "sausage tree".

'During the rainy season these trees, together with the thicket of shrubs and smaller trees such as *Markhamia acuminata*, *Commiphora stuhlmannii*, *Commiphora boiviniana*, *Grewia pachycalyx* and *Triaspis speciosa*, form a dense shade which completely excludes the growth of grasses and annual herbs except in glades along the bank of the stream and the forest wall, where we find also a tangle of *Acalypha ornata*, *Acacia pennata* and *Phyllanthus* shrubs.

'In the deep forest grow the fibrous leaves of *Sansevieria* spp. and succulent Euphorbias, while the forest above is tangled over with the climbing Combretums, *C. trichopetalum* and *C. obovatum*, and a host of Convolvulaceae.'

'Grass fires do not penetrate the riverine forests, whose shade is often sought by rhinoceros.'

'The soil is a deep brown or grey, non-cracking riverine silt, and is very good for crops.'

## 3. TABORA

The big rivers Igombe, Wala, Ugala and Rungwa support heavier vegetation of a semi-evergreen character, quite different from that just described from the thornbush country through which the Shinyanga rivers flow.

The commonest tree is *Syzygium guineense*, with pale, rather fleshy evergreen leaves and willow-like habit. Above the low canopy of these drooping trees stand tall *Diospyros mespiliformis*, and less numerous *Garcinia livingstonei* with yellow latex, *Ficus* spp., *Mimusops* sp., and *Gardenia*. The thicket below is composed of *Canthium queinzii*, *Antidesma venosum* and *Flacourtie ramontchi*, often with *Ochna stuhlmannii* and an unknown species of *Grewia* with round hairy leaves and large yellow flowers. Beneath this thicket mass grow frail *Psychotria* and the climbing *Paullinia pinnata*. In open spaces by the water's edge we find the low growing thorny *Mimosa asperata* with hairy fruits and pink flowers, and species of *Herminiera* (ambatch) and *Sesbania*. The large *Acacia*, *A. sieberiana*, occurs here and there, and in September many fish may be observed rising to take its fallen flowers.

Large permanent pools on these rivers contain hippopotamus and crocodile throughout the dry season.

## 4. MBEYA

'Riverine areas of rich brown alluvium are found along all the principal tributaries of the Ruaha and are dominated by large trees of *Acacia albida* (Phot. 51). These soils are much cultivated by the natives for maize crops and afford important dry season grazing.' On the west side of Mbeya in the Rukwa depression, 'the principal rivers are the Sira and Songwe, both flowing all the year round, and flanked by a variable width of large *Acacia albida* trees often confined to a flood plain lying in a 100 ft. deep gorge carved out by the river. The Sira is remarkable for its belt of *Phragmites communis* which may be over a quarter of a mile wide and which forms the dry season retreat of large herds of buffalo.'

On the Mbeya highlands above 6000 ft. patches of evergreen forest have survived the annual fires; but these forests have not been described by Burtt.

## 5. ABERCORN, NORTHERN RHODESIA

Swamp forest is found near the Lake shore at Mbete and Kituta bay. 'The forest is composed of gigantic trees, *Mitragyna*, *Syzygium*, *Chrysophyllum*, *Albizzia glabrescens*, *Ficus*, *Sorindeia* and *Elaeis* palms, the interlacing branches giving a cathedral effect. The ground is carpeted with decaying leaf litter except near small streams where a thick growth of *Amomum* conceals the water. Great buttress supports are usual on the larger trees.'

'The Lunzua river is flanked by a strip of evergreen riverine forest; this strip extends almost 29 miles along the course of the river. The forest is dominated by *Syzygium guineense*, *S. cordatum* and *Berlinia craibiana*, together

with *Gardenia imperialis*, *Mitragyna* sp. and Rubiaceous undershrubs including a wild species of coffee and many climbing plants. The forest is open-below and carpeted with leaf litter and fallen branches.

'Fringing forests of similar character are found along all the rivers and their tributaries in the Isoka, Abercorn and Mporokoso Districts. The forests may be fairly continuous, as along the Mululwe river and the tributaries of the Lufu; or they may be small scattered forests, near the sources of the rivers, often with tall raffia palms.'

#### 6. DOMIRA BAY, NYASALAND

'Riverine alluvial valleys occur along the flanks of all the rivers flowing towards Lake Nyasa. They are dominated by huge trees of *Acacia albida* (Phot. 51) with scattered *Acacia sieberiana*, *Acacia campylacantha*, *Ficus sycomorus* and *Cordyla africana*. These areas are composed of rich brown alluvium and are much sought after for the cultivation of food crops and cotton.'

'Along the courses of both seasonal and permanent rivers, especially where their valleys narrow and flow through *Brachystegia* woodland, we find a strip of dense riverine fringing forest flanked by deciduous thicket. The larger trees in the riverine forest are *Albizzia zygia*, *Ficus sycomorus*, *Mimusops densiflora*, *Parkia filicoidea*, *Piptadenia* cf. *africana*, *Tamarindus indica* and *Trichilia emetica*. Near Kotakota raffia palms, *Raphia vinifera*, were seen from the air to be scattered in riverine vegetation of a much denser type than that seen in the Domira Bay region.'

#### 7. THE CENTRAL PROVINCE

##### (i) Subtropical evergreen forest.

Relict patches of subtropical evergreen forest are found along the higher summits of the Bereku ridge north of Kondoa Irangi. From Burtt's diary notes I am able to construct the following short account of this vegetation type, which appears to occur from 6000 to 7000 ft.

The dominant trees are *Podocarpus gracilior* and *P. milanjianus*. Tree Ochnas and very large *Albizzia laevicorticata* are noticeable, and where fire has entered, especially in ravines, there is a thick tangle of brambles (*Rubus*) and bracken (*Pteridium aquilinum*), together with Vernonias. Areas of untouched forest are carpeted with leaf mould and a dwarf *Impatiens*. Towards the hill summits the undergrowth is chiefly ferns and Peperomias, and around the rocks of the actual summits, Ericaceous shrubs to 15 ft. and a giant *Impatiens* are dominant.

Other species noticed were *Apodytes dimidiata*, *Clausena* cf. *anisata*, *Myrsine africana*, *Calodendrum capense*, *Phoenix reclinata* (wild date palm), *Olea hochstetteri*, *Cassine croceum*, *Royena lucida*, *Euclea macroglossa*, *Psychotria capensis*, *Toddalia aculeata* (a liane), *Chrysophyllum* spp., a large tree *Conopharyngia* sp. and *Caesalpinia* cf. *bonduc*, a liane.

The only grass observed was *Oplismenus* sp.



Phot. 49. Savannah of *Borassus aethiopum* in western Singida (p. 121).



Phot. 50. *Hyphaene crinata* surrounding a dambo in Nyasaland, with the Rifu hills behind (p. 121).





Phot. 51. Riverine forest of *Acacia albida* in Nyasaland (pp. 119, 120).



Phot. 52. Heavy riverine forest strip in western Mwanza, with characteristic 'murram pavement' in foreground (p. 118).



In the east, subtropical evergreen forest is found near Mpwapwa from 5000 to 6100 ft. These forests occur as remnants of the original primaeval forest that at one time clothed a very much larger area of the mountain tops than they do today; the ravages of seasonal grass fires and the consequent exposure and removal of the humus by erosion have now reduced them to small areas on sheltered slopes, in ravines and on the mountain peaks themselves. Occasional isolated and aged forest trees still survive in the upland savannahs; they are clothed with epiphytes and surrounded by a thicket of secondary forest elements sheltering under the shade of the survivor, and protecting it from otherwise inevitable destruction.

The observer will notice at once the sharp wall of the surviving subtropical forest, where charred branches and stumps are tangled over by secondary forest thicket composed of *Cluytia*, *Vernonia podocoma*, *Rubus pinnatus*, bracken and coarse grasses; he will see on the lee side of the forest the advance guard striving to re-establish itself, composed of *Myrsine africana*, *Cluytia*, *Tecomaria shirensis*, evergreen Rubiaceous saplings and those of the forest elements themselves. In some parts of the upland savannah where large *Brachystegias* have for several years escaped the fires, colonisers from the subtropical evergreen forest have had the chance to establish themselves and would if left to their own devices engulf the invaders.

I did not see either of the *Podocarpus* trees which are such a feature of the surviving forests on the Berekü ridge north of Kondoa Irangi. The most conspicuous trees on the Kiboriani mountains are *Albizzia gummifera*, *Calodendrum capense*, *Cussonia spicata*, *Apodytes dimidiata* and occasional *Phoenix reclinata*.

#### (ii) Riverine communities.

The riverine forests of the Central Province are generally similar to those already described for Shinyanga in the Lake Province, but in addition there may be palm forests along the rivers, and additional elements where, as near Mpwapwa, the river runs all the year round.

Near Kazikazi, for example, both *Borassus* palm and *Piptadenia* fringing associations are found. Where the railway climbs the Rift Wall, 'the Hika and Ruwiri rivers are both fringed with thick riverine forest dominated by *Piptadenia hildebrandtii*, with *Acacia usambarensis* and *Tamarindus indica*; *Lonchocarpus capassa* and *Kigelia aethiopica* are very common.'

The riverine forests resemble those at Kazikazi and Shinyanga but in places differ from them in the presence of large numbers of the spectacular feather palm *Hyphaene crinata* (Phot. 50). Near Hika these palms form an almost pure stand, while on the alluvial plains below the Kilimatinde scarp they occur in great profusion.'

(a) *Palm communities.* Of the *Borassus aethiopum* riverine strips (Phot. 49), Burtt writes: 'Their majestic trunks tower 70 ft. or more above the ground.

Two thirds of the way up, the trunks are swollen with a bottle like protuberance which marks the spot at which the palm began to flower and produce its enormous fruits. These are the size of a football and, when ripe, have a strong pineapple scent which greatly belies their stringy texture and unsavoury flavour. The fruits are sought after by elephant which after chewing them spit out or accidentally swallow the seed, thereby distributing them afar. Those who have camped in the *Borassus* forest will always remember their majestic shapes silhouetted in the lurid sunset in the dusk, and the fury of the crashing of the giant leaves when buffeted by storms. In the dry season, fires rage through the palm forest, here and there catching the dead leaves of a small palm which soon blazes up, a gigantic pillar of fire devouring the green fronds and leaving only a charred skeleton: the trees however are admirably adapted for this severe treatment and soon recover, none the worse for their fiery adventure.'

(b) *Acacia xanthophloea* communities. Another type of riverine vegetation is the *Acacia xanthophloea* forest. These are the 'fever trees' of Kipling's 'great, greasy Limpopo'. This type is absent from the Lake Province but common in the Central and Northern Provinces, notably in the valleys of rivers flowing off the Rift escarpment into Lake Manyara and along the Bubu river. 'So far I have not seen "fever tree" forest in the area west of Lake Eyasi, the Wembere or Singida District. In the Southern Highlands Province, it occurs round Lake Rukwa.

'Rivers and lake shores are clothed with a woodland of tall yellow, powdery barked Acacias, *A. xanthophloea*. The trees grow to 60 ft. in height and form an open woodland in which the moist alluvial soil often encourages exceptionally tall and impenetrable jungle of *Phragmites communis*, *Sorghum arundinaceum*, *Panicum maximum* and a tall lacerating reed *Cyperus grandis* (?). Where the grasses are shorter there are tangles of *Achyranthes aspera* and impenetrable thickets of *Microglossa densiflora* may be common. Here and there are thickets of *Combretum trichopetalum* and *Ximenia americana* both of which climb high up into the Acacias.

'The "fever tree" forests are usually burnt out by seasonal grass fires which result in luscious grazing for cattle in the early rains where the forests are free from tsetse.

'Reedbuck, roan, impala, eland, waterbuck and zebra have been seen in the forests, and elephant pass through them at certain seasons of the year. In the Lake Manyara region hippo trails and buffalo spoor are frequent in the forest.

'The soil is grey or brown riverine silt of considerable depth.'

(c) *Mpwapwa* riverine communities. Riverine forest of a different kind 'occurs locally as a narrow strip along permanent rivers such as the headwaters of the Tubugwe and Kikombo rivers which drain off the Mpwapwa hills, and no doubt would be found on the western slopes of the Nguru and Kaguru mountains.'

'After travelling in the heat of the dry season noonday sun through miles of leafless *Brachystegia* or *Acacia tortilis* woodland and blazing patches of bare cultivation, the cool shade of the riverine forest is exceedingly comforting. Near Mpwapwa several streams flow from the mountain passes throughout the year, but after a few miles they disappear underground or are evaporated. The dense wall of tall forest that fringes the stream stands out like a green snaky ribbon in the burnt-up country when viewed from the mountains or from an aeroplane.

'Approaching the forest on foot our attention will be drawn to an occasional giant *Khaya* tree whose dark green massive canopy rides above the wall of the forest; unfortunately few of them are spared by the woodman's axe. Entering the forest we find its dark shade supporting ferns and a carpet of dark green leaves of *Culcasia scandens*, while the banks of the cool stream of crystal clear water are shaded by large trees of *Ficus vallis-choudae*, *Ficus sycomorus*, *Ziziphus mucronata*, *Albizia gummifera*, *Albizia glabrescens*, *Trichilia emetica*, *Parkia filicoidea*, *Combretum schumannii*, *Commiphora zimmermannii* etc.

'Great lianes hang across the forest shade—an evergreen *Strychnos* or *Combretum abbreviatum*, the latter covering the forest crown with flaming red masses of its flowers in season. In places during the dry season, we may find the enormous scarlet flowers of *Ferdinandia magnifica*, a Bignoniaceous tree fairly common on the coast.

'The outer wall of the forest is choked with a massive growth of *Disperma*, *Acalypha engleri* and rank herbage which keeps out the dry season grass fires.

'The forest shade is a favourite resort of bushpig, greater kudu, and in the dry season buffalo, which come down from the mountains to drink and to lick the salty crust of the stream.

'The rich humus surface soil is several inches deep and covered with leaf litter. Where the river valley is narrow, a gorge is cut into the red soils of the hillside.

'The riverine fringing forests of Mpwapwa vary in composition with altitude. In the sheltered higher valleys they resemble rain forest, with very large trees. A few huge *Khaya* trees remain with large *Ficus vallis-choudae*, *Albizia gummifera*, *Trichilia emetica*, and *Sorindeia obtusifoliolata*, forming a dense canopy above a scanty covering of the well known forest herbs *Desmodium scalpae*, *Oplismenus hirtellus*, *Impatiens hochstetteri* and ferns. In the upper riverine fringing forests we find large trees of *Acacia campylacantha*, and a few candelabra Euphorbias and *Acacia tortilis* that have been engulfed by the advancing forest margin which is choked with *Acalypha ornata* and *Disperma crenata*.

'Near Mpwapwa the riverine fringing forest is dominated by large riverine Acacias, the principal species being *Acacia albida*, *A. campylacantha*, and *A. tortilis*. Large trees of *Kigelia aethiopica*, *Lonchocarpus capassa* and *Tamarindus indica* are frequent. The herbaceous canopy is suppressed by an impene-

trable tangle of *Acacia pennata*, *Harrisonia abyssinica*, *Helinus ovatus*, *Plumbago zeylanica* and *Disperma crenata*, the last forming thicket to 7 ft. in height. *Panicum maximum* with *Wedelia* and *Achyranthes aspera* are common in the glades or forest margin.

'In the lower riverine fringing forest at Gulwe large baobabs are common, with *Terminalia aemula*, *Tamarindus*, *Ficus sycomorus* and *Ziziphus mucronata*. The herb stratum is entirely suppressed by thicket of *Dombeya cincinnata*, *Hippocratea obtusifolia*, Grewias, *Rothmannia* sp., *Acacia pennata*, *Rhus*, *Triaspis speciosa* and *Uvaria*.'

#### 8. THE LUKOSI VALLEY AREA, USAGARA

'From the foot of the Katonga pass as far as Mrugira the riverine strip is very narrow, being for the most part only "one tree width" on either bank. It is dominated by large trees of *Pterocarpus*, *Albizia glabrescens*, *Adenia globosa*, *Erythrophloeum guineense*, *Parkia filicoidea*, *Ficus sycomorus*, *Rauvolfia inebrians* and *Terminalia aemula*. *Lonchocarpus capassa*, *Kigelia aethiopica*, *Acacia usambarensis* and *Acacia albida* fringe the riverine area where the gorge widens out; further down, the riverine forest is dominated by *Piptadenia hildebrandtii* and *Albizia glabrescens* interspersed with *Acacia albida*, *Acacia tortilis*, *Tamarindus indica* and *Trichilia emetica*. The floor is covered with decaying leaf litter which supports a thin carpet of Acanthaceous herbs, and here and there are groves of *Euclea kellaui* forming thicket.'

'Towards the Ruaha the riverine forest becomes dominated by *Acacia albida* with, near the Ruaha, dense thicket tangle of *Cordia gharaf*'.

#### 9. THE EASTERN PROVINCE (MOROGORO)

'The Ngerengere river about 14 miles from Morogoro passes close to the station of Kingolwira flowing west to east and then swinging almost due north for about 10 miles, passing the isolated hills of Mkumbu and Mbokwa before turning eastwards again in a wide curve. Here it passes through dry *Combretum-Acacia nigrescens* savannah (Phot. 48). This savannah is broken by dry thicketed tributary gulleys largely covered with *Acacia pennata* with scattered candelabra Euphorbias and an impenetrable undergrowth of *Sansevieria* spp. The river is hidden by a thick evergreen gallery or fringing forest of large trees 80 to 100 ft. high. The width of the forest is about 200 yards.'

'The principal trees are *Albizia glabrescens*, *Albizia gummifera*, *Albizia brachycalyx*, *Acacia campylacantha*, *Acacia usambarensis*, *Parkia*, *Khaya senegalensis*, *Ficus sycomorus*, *Sterculia appendiculata*, *Kigelia aethiopica*, *Trichilia emetica* and rare *Raphia* and *Borassus* palms. Under the large trees are found those demanding shade; *Chrysophyllum msolo*, *Sorindeia obtusifoliolata* and *Conopharyngia*.

'The forest is shut in by a wall of climbers, chiefly *Landolphia kirkii*, *Dalbergia arbutifolia*, *Paullinia pinnata*, *Smilax* and *Combretum abbreviatum*, with undergrowth of *Acalypha engleri* and pepper.

'In the deep shade there is no grass but a carpet of dark green leaves of *Culcasia scandens*, while under the densest thickets the ground is covered with leaf mould and rotting twigs.'

### VIII. TERMITE MOUND COMMUNITIES

'These are found throughout the area in the broad leaved deciduous woodland, the deciduous *Acacia* thorn country and the riverine fringing forest. Termite mounds are however most abundant in the Itigi thicket, the interzone between Itigi thicket and miombo, the *Combretum zeyheri-Ostryoderris stuhlmannii-Terminalia sericea* woodland of the Central and Lake Provinces, and in the hard pan country.

'Termite mounds form one of the most familiar features of the Central Plateau scenery. They are usually low mounds raised 4 or 5 ft. above the general level of the ground and having a base 10 to 12 ft. in diameter. Some mounds have ventilation shafts, which may be built into earthen chimneys a foot or two above the top of the mound.

'A glance at the air photographs of the Itigi thicket shows a great number of denser mottlings some of which are broken by a white centre. These are all termite mounds, the white marks being the tops of fresh mounds with chimneys (Phot. 45).

'The soil of termite mounds sets exceedingly hard in the dry season, but in the rains the finely divided clayey structure becomes evident, and the surface has an oily slipperiness after showers. Sprinkling dilute hydrochloric acid on large termite mounds often produces strong effervescence indicating the presence of lime. This may be noticed on mounds situated in definitely acid soils and suggests that the lime may have been brought to the surface by the termites from considerable depths.

'The limy factor may be responsible for the thicket vegetation which so often covers termite mounds. Thickets which in country of normal grass fires confine themselves entirely to the wash from the mound are composed of definite hard pan elements such as *Commiphora schimperi*, *Lannea humilis*, *Cassia singueana*, *Albizia harveyi*, *Grewia bicolor* and *Grewia praecox*. The shade produced by these plants is then favourable for the growth of certain thicket frequenting species such as *Markhamia acuminata*, *Maerua angolensis* and *Commiphora stuhlmannii*, while on many termite mounds we find the candelabra Euphorbia (*E. bilocularis*), *Ziziphus mucronata* and even an occasional *Tamarindus indica* or baobab.

'It must not be forgotten that the age of termitaria may be immense, large ones being the result of successive piling up of finely divided clays for centuries.

Tall mounds offer perching places for birds and a refuge for a whole host of small mammals. By the agency of both mammals and birds seed dispersal is effected, and the necessary thicket shade together with protection from grass fires soon enables plants to grow which otherwise would have perished. The thickets on several termitaria situated in close proximity to one another may in years coalesce to form one island thicket; this has been suggested by the formations of certain hard pan thickets seen at Kazikazi and elsewhere.'

Burtt was preparing a fuller account of the termite mounds and the plant communities which live on them, but this was only just started. In the Tabora miombo I analysed the woody plants of a fairly large number of termitaria, and am able to add the following notes.

Common large trees on the termite mounds are *Ficus* sp., *Albizia harveyi*, *A. amara* and *A. brachycalyx*, *Berchemia discolor*, *Mimusops densiflora*, *Tamarindus indica*, *Ziziphus mucronata* and *Z. mauritiana*, *Acacia usambarensis*, *Diospyros mespiliformis* and *Euphorbia bilocularis*. Rather smaller species include *Boscia pachysandra*, *Balanites tomentosa*, *Cassia abbreviata* and *C. siingueana*, *Capparis kirkii*, *Strychnos heterodoxa*, *Fagara merkeri*, *Teclea glomerata*, *Tricalysia cacondensis*, *Lonchocarpus eriocalyx* and *L. capassa*. Still smaller trees are *Commiphora subsessilifolia*, *C. stuhlmannii* and *C. pilosa*, *Canthium* sp. and *Strophanthus eminii*.

Shrubs are of course numerous, including about half a dozen scented species of which *Premna* and *Clerodendron* may be mentioned; non-scented species include *Allophylus africanus* and *A. griseo-tomentosus*, *Bridelia ferruginea* and *B. fischeri*, *Grewia platyclada* and *G. bicolor*, *Popowia obovata*, *Ehretia caerulea* and *Ximenia*.

Climbers are *Acacia pennata*, *Plumbago zeylanica*, *Desmonema mucronulatum*, *Fockea schinzii*, *Cissus* sp., *Combretum obovatum* and *Hippocratea obtusifolia*.

Of these plants, *Diospyros mespiliformis* and *Ziziphus mauritiana* are scarce or absent in the Central and Lake Provinces.

In Musoma District of the Lake Province the principal thicket elements on the termite mounds (Phot. 32) are *Harrisonia abyssinica*, *Rhus glaucescens*, *Grewia bicolor* and *Acacia pennata*, with a 'bayonet' *Sansevieria* growing below. In the Shinyanga area there is a much greater profusion of species, and the genus *Grewia* is especially well represented.

#### IX. TABLE SHOWING DISTRIBUTION OF SPECIES

The first column contains the name of the species and the author's name, the second an abbreviation indicating the most characteristic type in which the species occurs. Where the species is not specially found in any one particular type, this second column is left blank.

The remaining columns show the distribution in the different parts of the

country considered, and are divided into two groups. Group 1 represents the southward transect from Lake Victoria to Lake Nyasa, and Group 2 the south-eastward transect to the coastal plain. The records have been filled in partly from the foregoing descriptions by Burtt himself, partly from notes in his catalogue of plants collected, and partly from my own and Mr Potts's experience. It will therefore be appreciated that, though a blank column often indicates that a species is rare or absent, this conclusion will not be invariably correct.

The problem of selection has been a very difficult one. I have, however, omitted all grasses and herbs, and tried to select only the more important genera.

The species given under the difficult genera *Commiphora* and *Brachystegia* are those recognized in Burtt's and my papers, and other names have been amended in accordance with Eggeling (1940) cited in the references at the end.

Abbreviations used in the 'habitat' column are:

C	<i>Combretum</i> savannah	M	<i>Isoberlinia</i> - <i>Brachystegia</i> savannah)	R	riverine
E	evergreen forest	P	<i>Protea</i> highland grassland	S	seasonal swamp
Hp	hard pan			Th	thicket

Abbreviations in the remaining columns are:

c. common	c.-d. co-dominant	d. dominant
f. fairly or frequent, according to context	l. local(ly)	r. rare v. very

As some of the name changes which I have taken from Eggeling's book may be unacceptable or unfamiliar to many East African botanists, I think it best to give a list of them here, so that species with new names may be readily found in the Table.

Old name	New name
<i>Acacia</i> nefasia Schweinf.	<i>Acacia</i> sieberiana DC.
<i>A. spirocarpa</i> Hochst.	<i>A. tortilis</i> (Forsk.) Christensen nec Hayne
<i>A. stenocarpa</i> Hochst.	<i>A. holstii</i> Taub.
<i>Amblygonocarpus schweinfuerthii</i> Harms.	<i>Amblygonocarpus obtusangulus</i> Harms.
<i>Borassus flabellifer</i> Warb.	<i>Borassus aethiopum</i> Mart.
<i>Clausena</i> inequalis Benth.	<i>Clausena anisata</i> (Willd.) Oliv.
<i>Combretum fischeri</i> Engl.	<i>Combretum binderanum</i> Kotschy.
<i>C. ternifolium</i> Engl. & Diels.	<i>C. ghasalense</i> Engl. & Diels.
<i>Cordia holstii</i> Gürke.	<i>Cordia abyssinica</i> R.Br.
<i>C. rothii</i> Schm.	<i>C. gharaf</i> (Forsk.) Ehrenb.
<i>Dombeya reticulata</i> Mast. and Dombeya rotundifolia Harv.	<i>Dombeya quinqueseta</i> (Del.) Excell.
<i>Erythrina tomentosa</i> R.Br.	<i>Erythrina abyssinica</i> Lam.
<i>Heeria insignis</i> O. Ktzh.	<i>Heeria reticulata</i> (Bak. f.) Engl.
<i>Rhus villosa</i> L. f.	<i>Rhus incana</i> Mill.
<i>Sesbanea aegyptiaca</i> Poir.	<i>Sesbanea sesban</i> (L.) Merr.
<i>Strychnos burtonii</i> Bak.	<i>Strychnos innocua</i> Del.
<i>Syzygium owariense</i> Benth.	<i>Syzygium guineense</i> DC.
<i>Veronia senegalensis</i> Less.	<i>Veronia colorata</i> Drake
<i>Vitex cienkowskii</i> Kotch. & Peyr.	<i>Vitex cuneata</i> Thonn.
<i>Ziziphus jujuba</i> Lam.	<i>Ziziphus mauritiana</i> Lam.



<sup>†</sup> Also found at Kahama.

#### \* Near A. ulugurensis.

Habitat (Shinyanga) (S. Tabora)	Group 1		Group 2		Eastern Province (Kilosa, Morogoro)
	Lake Province	Southern Province (Mbeya)	Nyassaland (Bua River Bay)	Western Province (Mbeya)	
<i>Brachystegia boehmii</i> Taub.	M	l.d.	c.	c.	d.
<i>B. burttii</i> Hoyle (MS.).	M	l.d.	l.d.	l.d.	i.c.
<i>B. bussei</i> Harms.	M	l.	l.	l.	l.
<i>B. floribunda</i> Benth.	M	l.d.	l.d.	l.d.	.
<i>B. longifolia</i> Benth.	M	l.d.	c.-d.	c.-d.	.
<i>B. microphylla</i> Harms.	M	l.d.	c.-d.	c.-d.	.
<i>B. spiciformis</i> Benth.	M	v.l.	v.e.	l.d.	f.f.
<i>B. stipulata</i> De Wild.	M	l.	l.d.	c.-d.	l.d.
<i>B. taxifolia</i> Harms.	M	l.	l.d.	c.	l.d.
<i>B. utilis</i> Hutch. & Burtt Davy	M	v.l.	l.c.	f.	l.d.
<i>B. wangermeana</i> De Wild.	M	f.	f.	f.	l.
<i>Bridelia ferruginea</i> Benth.	M	f.f.	f.e.	f.	l.
<i>B. fischeri</i> Pax.	R	l.	f.c.	f.c.	l.
<i>B. micrantha</i> (Hochst.) Baill.	M	c.	f.	f.	f.f.
<i>Burkea africana</i> Hook.	Th	v.r.	l.	l.	r.
<i>Burtia pruinoides</i> Bak. f. & Exell.	Th	..	..	..	f.f.
<i>Bussea massaiensis</i> Harms.	Th	..	..	..	v.c.
<i>Byrsocarpus maximus</i> Bak.	Th	..	..	..	v.c.
<i>Cadaba adenotricha</i> Gilg. & Benth.	Hp	c.	c.	c.	c.
<i>C. farinosa</i> Forsk.	Th	..	..	..	c.
<i>C. kirki</i> Oliv.	Hp	..	c.	c.	c.
<i>C. obovata</i> E. A. Br.	Hp	..	..	..	l.c.
<i>C. stenorhoda</i> Gilg. & Benth.	Hp	..	..	..	l.c.
<i>Cæsalpinia</i> cf. <i>bondue</i> Roxb.	E	..	..	..	..
<i>C. trothae</i> Harms.	Th	..	..	..	..
<i>Calodendrum capense</i> Thunb.	E	..	..	..	..
<i>Caethalium burttii</i> Bulllock	M	r.	f.c.	f.	f.
<i>C. crassum</i> Hiern.	R	r.	c.	f.	f.
<i>C. gneimii</i> Sond.	M	c.	f.c.	f.	f.
<i>C. hillense</i> Hiern.	Th	..	r.	r.	f.
<i>Canthium</i> sp. (?) <i>lactescens</i> Hiern.)	Hp	..	c.	f.r.	l.c.
<i>Capparis elaeagnoides</i> Gilg.	Th	f.f.	..	f.c.	..
<i>C. filacina</i> Gilg.	Th	f.f.	..	f.f.	f.f.
<i>C. kirki</i> Oliv.	Hp	..	c.	..	f.c.
<i>C. tomentosiss.</i> Lam.	M	..	c.	f.	f.
<i>Carpodiptera africana</i> Mast.	..	..	..	..	f.f.
<i>Cassia abbreviata</i> Oliv.	..	..	..	..	f.r.
<i>C. auriculata</i> L.	..	..	..	..	f.f.
<i>C. burttii</i> Bak. f.	..	..	..	..	l.
<i>C. didymobotria</i> Friesen.	Th	..	..	..	l.f.



Habitat (Shinyanga) (S. Tabora) (Mbeaya)	Group 1		Group 2		Eastern Provinces (Kilosa, Morogoro)			
	Lake Province	Western Province	Southern Highlands Province	Nyassaland (Bu River Bay)	Central Province (Manyoni)	Central Province (Kondoa)	Central Province (Domira)	Central Province (Kilosa, Morogoro)
<i>C. transvaalense</i> Schinz.	C	f.	v.r.	.	f.	f.	c.	l.c.
<i>C. trichopetalum</i> Engl.	R	f.	v.j.	.	f.	f.	c.d.	l.d.
<i>C. trothae</i> Engl. & Diels.	Th	v.e.	v.e.	l.c.	v.c.	v.c.	v.c.	v.c.
<i>C. zeyheri</i> Sond.	C	v.e.	v.e.	f.	.	.	.	.
<i>Combretum cf. zeyheri</i> Sond.	R	f.f.	.	l.c.	.	.	.	.
<i>Commiphora boiviniana</i> Engl.	Th	v.l.	.	l.c.	f.c.	f.c.	f.f.	f.f.
<i>C. caerulea</i> B. D. Burtt	HP	l.d.	.	l.c.	c.	c.	v.o.	v.o.
<i>C. campestris</i> Engl.	HP	l.d.	.	l.c.	c.	c.	c.	c.
<i>C. emini</i> Engl.	C	c.	c.	l.	c.	c.	c.	c.
<i>C. fischeri</i> Engl.	Th	v.e.	c.	l.	c.	c.	c.	c.
<i>C. hornbyi</i> B. D. Burtt	Th	.	c.	l.	c.	c.	c.	c.
<i>C. kimbilensis</i> Engl.	Th	f.	c.	l.c.	c.	c.	c.	c.
<i>C. laxiflora</i> Engl.	Th	.	c.	l.c.	c.	c.	c.	c.
<i>C. merkeri</i> Engl.	Th	.	c.	l.c.	c.	c.	c.	c.
<i>C. mollis</i> Engl.	M	v.e.	c.	l.	c.	c.	c.	c.
<i>C. pilosa</i> Engl.	Th	v.e.	c.	l.	c.	c.	c.	c.
<i>C. pteleifolia</i> Engl.	HP	f.c.	c.	l.	c.	c.	c.	c.
<i>C. pugnans</i> Engl.	HP	c.-d.	f.	l.c.	c.	r.	r.	r.
<i>C. sarandensis</i> B. D. Burtt	HP	l.	f.	l.c.	c.	f.	f.	f.
<i>C. schimperi</i> Engl.	HP	l.	f.	l.c.	c.	f.	f.	f.
<i>C. stolonifera</i> B. D. Burtt	HP	l.	f.	l.c.	c.	f.	f.	f.
<i>C. stoltzii</i> Engl.	Th	l.	f.	l.c.	c.	f.	f.	f.
<i>C. stuhlmannii</i> Engl.	HP	e.	f.	l.c.	c.	f.	f.	f.
<i>C. subsessilifolia</i> Engl.	HP	v.c.	f.f.	l.c.	c.	f.	f.	f.
<i>C. swynnertonii</i> B. D. Burtt	HP	l.c.	f.f.	l.c.	c.	f.	f.	f.
<i>C. ugogenensis</i> Engl.	C	v.c.	l.c.	l.c.	c.	f.	f.	f.
<i>C. zanzibarica</i> (Baill.) Engl.	R	l.c.	v.c.	v.c.	c.	f.	f.	f.
<i>C. zimmermannii</i> Engl.	R	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Conopharyngia</i> sp.	E	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Cordia abyssinica</i> R. Br.	R	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>C. ghafra</i> (Porsk.) Ehrenb.	Th	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>C. ovalis</i> R. Br.	Th	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Cordia n.sp.</i>	Th	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Cordyla africana</i> Lour.	Th	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Courtonia edulis</i> Gilg. & Benth.	Th	l.c.	l.c.	l.c.	c.	f.	f.	f.
<i>Craibia burttii</i> Bak.	Th	c.	c.	c.	c.	c.	c.	c.
<i>Crosopteryx febrifuga</i> Benth.	C	v.r.	v.r.	v.r.	c.	c.	c.	c.
<i>Croton dichogamus</i> Pax.	Th	f.	f.	f.	c.	c.	c.	c.
<i>C. macrostachys</i> Hochst. ex A. Rich.	Th	l.c.	l.c.	l.c.	c.	c.	c.	c.
<i>C. polytrichus</i> Pax.	Th	l.c.	l.c.	l.c.	c.	c.	c.	c.



	Habitat (Shinyanga) (S. Tabora) (Mboya) (Abercorn)	Group 1		Group 2						Eastern Province (Kilosa, Mpwapwa, Morogoro)	
		Lake Province	Southern Highlands Province	Nyassaland (Bua River Bay)	Northern Rhodesia and Domira Province	Central Province (Manyoni)	Central Province (Kondoa)	Central Province (Mtwara)	Central Province (Tanga)	Central Province (Zanzibar)	
<i>Euphorbia mataleensis</i> Pax.	Th	.	.	f.	.	f.c.	I.c.	f.	.	c.	.
<i>E. nyikae</i> Pax.	M	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Euphorbia cf. strangulata</i> N. E. Br.	Hp	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Pagara merkeri</i> Eng.	Th	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. trijuga</i> Dunkley	C	.	.	f.	.	f.c.	f.c.	f.	.	f.	.
<i>F. xanthoxyloides</i>	M	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Faurea argentea</i> Hutch.	M	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. speciosa</i> Welw.	P	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Ferdinandia magnifica</i> Seem.	R	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Feretia</i> n.sp.	Hp	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>Ficus exasperata</i> Vahl.	R	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. gnatophocarpa</i> A. Rich.	R	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. nigropunctata</i> Warb.	Th	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. populifolia</i> Vahl.	Th	.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. sonderi</i> Miq.	R	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. stuhlmannii</i> Taub.	R	l.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. subcalcarata</i> Warb.	R	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. sycomorus</i> L.	R	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. vallis-choudae</i> Del.	R	c.	.	f.	.	f.c.	f.c.	f.	.	f.f.	.
<i>F. wakefieldii</i> Hutch.	M	r.	c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Flacouria ramontchi</i> L'Herit.	Th	r.	c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Phlegia viriss.</i> Baill.	Th	r.	c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Fockea schinzii</i> N. E. Br.	R	r.	c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Garcinia livingstonei</i> T. And.	R	r.	c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Gardenia imperialis</i> K. Schum.	Th	r.	v.c.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. resiniflora</i> Hiern.	R	c.	v.l.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. thunbergia</i> L. f.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>Grewia bicolor</i> Juss.	R	c.	v.l.	f.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. burttii</i> Exell.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. dumicola</i> Exell sp.nov.	Th	c.	v.l.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. fallax</i> K. Schum.	R	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. forbesii</i> Harv.	Th	c.	v.l.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. glauca</i> Exell.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. microcarpa</i> K. Schum.	HP	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. mollis</i> Juss.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. monticola</i> Sond.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. oncopetala</i> K. Schum.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. pachycalyx</i> K. Schum.	R	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. platyclada</i> K. Schum.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.
<i>G. praecox</i> K. Schum.	Th	c.	v.c.	v.c.	r.	f.c.	f.c.	f.	.	f.f.	.



	Group 1		Group 2		Eastern Provinces (Kilosa, Morogoro)			
	Lake Province	Habitat (Shinyanga) (S. Tabora)	Southern Province	Western Province	Nyasaland (Bua River Bay)	Northern Province (Rhodesia and Domira) (Abercorn) (Mbeya)	Central Province (Manyoni) (Kondoa)	Central Province (Kondoa) (Mpwapwa)
<i>Lannes fulva</i> Engl.	Th	c.	v.c.	v.c.	-	-	r.	f.
<i>L. humilis</i> Engl.	Hp	c.d.	c.	c.	-	-	c.-d.	f.
<i>L. schimperi</i> Hochst.	M	f.f.	-	-	-	-	v.c.	v.c.
<i>L. stuhlmannii</i> Engl.	Th	f.f.	-	-	-	-	f.c.	c.
<i>Lantana salviifolia</i> Jacq.	P	f.f.	-	-	-	-	f.f.	c.
<i>Lesiosiphon eminii</i> Engl. & Gilg.	Th	-	-	-	-	-	l.f.	l.f.
<i>L. glandeos</i> Fresen.	P	-	-	-	-	-	f.c.	f.c.
<i>L. mollissimus</i> E. A. Br.	M	-	-	-	-	-	c.	c.
<i>Lippia asperifolia</i> Rich.	R	f.	f.	f.	-	-	l.e.	l.e.
<i>Lonchocarpus capassa</i> Rolf.	f.	f.	f.	f.	-	-	f.f.	f.f.
<i>L. eriocalyx</i> Harms.	c.	-	-	-	-	-	c.	c.
<i>L. fischeri</i> Harms.	-	-	-	-	-	-	c.	c.
<i>L. pallescens</i> Welw.	-	-	-	-	-	-	f.r.	f.r.
<i>L. scheffleri</i> Bak. f.	-	-	-	-	-	-	l.c.	l.c.
<i>L. 'schimperi'</i>	-	-	-	-	-	-	-	-
<i>Maba abyssinica</i> Hiern.	Th	f.	f.	f.	-	-	f.f.	f.f.
<i>Maniekeria sulcata</i> Dubard.	Th	-	-	-	-	-	c.	c.
<i>Maerua angolensis</i> DC.	Hp	-	-	-	-	-	c.	c.
<i>M. crassifolia</i> Forsk.	Th	l.c.	l.c.	l.c.	f.c.	-	f.f.	f.f.
<i>M. flagellaria</i> Gilg. & Benth.	Th	l.c.	l.c.	l.c.	-	-	l.c.	l.c.
<i>M. hochneili</i> Schweinf.	Hp	l.f.	l.f.	l.f.	-	-	f.c.	f.c.
<i>M. johannis</i> Gilg. & Volkens.	M	l.c.	l.c.	l.c.	-	-	v.c.	v.c.
<i>M. nervosa</i> Oliv.	Th	-	-	-	r.	-	c.	c.
<i>M. sphaerogetyna</i> Gilg. & Benth.	Hp	-	-	-	r.	-	c.	c.
<i>M. trichophylla</i> Gilg.	M	v.c.	v.c.	v.c.	-	-	c.	c.
<i>Maprounea glauca</i> Hutch.	Th	v.c.	v.c.	v.c.	-	-	c.	c.
<i>M. acuminata</i> K. Schm.	Th	v.c.	v.c.	v.c.	-	-	c.	c.
<i>M. obtusifolia</i> Sprague	Th	c.	c.	c.	-	-	c.	c.
<i>Marsdenia umbellifera</i> K. Schm.	Hp	r.	r.	r.	-	-	l.c.	l.c.
<i>M. zambiana</i> Schltr.	R	-	-	-	-	-	l.c.	l.c.
<i>Microglossa densiflora</i> Hook. f.	R	-	-	-	-	-	f.f.	f.f.
<i>M. oblongifolia</i> O. Hoffm.	R	-	-	-	-	-	c.	c.
<i>Mimosa asperata</i> L.	R	-	-	-	-	-	c.	c.
<i>Mimusa densiflora</i> Engl.	R	-	-	-	-	-	f.	f.
<i>M. fruticosa</i> Boj.	R	-	-	-	-	-	c.	c.
<i>Monotes adenophyllum</i> Gilg.	M	-	-	-	-	-	c.	c.
<i>M. africanus</i> Welw.	M	-	-	-	-	-	l.c.	l.c.
<i>M. delevoyi</i> De Wild.	M	-	-	-	-	-	l.c.	l.c.
<i>M. discolor</i> R. E. Fries	R	-	-	-	-	-	l.c.	l.c.
<i>M. elegans</i> Gilg.	M	-	-	-	-	-	l.c.	l.c.

<i>M. engleri</i> Gilg.	
<i>M. homblei</i> De Wild.	
<i>M. katangensis</i> De Wild.	
<i>M. magnificum</i> Gilg.	
<i>M. rufotomentosum</i> Gilg.	
<i>Mundulea sericea</i> (Wild.) A. Chev.	
<i>Myrica salicifolia</i> Hochst. ex A. Rich.	
<i>Myrsina africana</i> L.	
<i>Myroxyon aethiopicum</i> Loes.	
<i>Obetia pinnatifida</i> Bak.	
<i>Ochna longipes</i> Bak.	
<i>O. macrocarpa</i> Engl.	
<i>O. stuhlmannii</i> Engl.	
<i>Ochna</i> n.sp.	
<i>Olea hochstetteri</i> Bak.	
<i>Opilia campestris</i> Engl.	
<i>Ornocarpum aromaticum</i> Bak. f.	
<i>O. kirii</i> S. Moore	
<i>O. trichocarpa</i> Harms.	
<i>Ostydroderris stuhlmannii</i> (Taub.) Dunn.	
<i>Osyris abyssinica</i> Hochst.	
<i>Oxytenanthera abyssinica</i> Munro	
<i>Paravaea dactylophylla</i> Welw.	
<i>Pappea ugandensis</i> Bak. f.	
<i>Parinari curatellifolia</i> Planch.	
<i>Parkia filicoidea</i> Welw. ex Oliv.	
<i>Paulinia pinnata</i> L.	
<i>Pavetta assimilis</i> Sond.	
<i>P. crassipes</i> K. Schm.	
<i>P. grandifolia</i> Korth.	
<i>P. oliveriana</i> Hiern.	
<i>P. rhodesiaca</i> Brem.	
<i>P. schumanniana</i> F. Hoffm.	
<i>Philippia benguelensis</i> Alm. & Th. Fries	
<i>Phoenix reclinata</i> Jacq.	
<i>Phyllanthus discoideus</i> Mull. & Art.	
<i>P. engleri</i> Pax.	
<i>P. fischeri</i> Pax.	
<i>P. reticulatus</i> Poir.	
<i>Piptadenia</i> cf. <i>africana</i> Hook. f.	
<i>P. hildebrandtii</i> Vatke	
<i>Pleurostylis africana</i> Loes.	
<i>Plumbago zeylanica</i> L.	
<i>Podocarpus gracilior</i> Pilgr.	
<i>P. milanjianus</i> Rendle	
<i>Popowia obovata</i> (Bkh.) Engl. & Diels.	

## Some East African vegetation communities

Habitat (Shiriyanga) (S. Tabora) (M. Mbeya)	Group 1		Group 2		Eastern Province (Kilosa, Morogoro)				
	Lake Province	Western Province	Southern Highlands	Nyassaland (Bua River Bay)	Northern Province	Rhodesia and Domira	Central Province (Manyoni)	Central Province (Kondoa)	Central Province (Mpwaspwa)
<i>Premna angolensis</i> Gürke	Th	f.f.	·	·	·	·	·	·	c.
<i>Protea abyssinica</i> Wild.	P	·	·	·	·	·	·	v.c.	·
<i>P. angolensis</i> Welw.	P	·	·	·	·	·	·	f.f.	·
<i>P. chilonantha</i> Engl. & Gilg.	P	·	·	·	·	·	·	v.c.	·
<i>P. madagascariensis</i> Oliv.	M	·	·	·	l.c.	·	·	·	·
<i>P. ulrichensis</i> Eng.	P	·	·	·	c.	·	·	v.c.	·
<i>Pseudolachnostylis maprouneaeifolia</i> Pax.	M	·	·	·	c.	·	·	f.f.	·
<i>Pseudoprosopis fischeri</i> Harms.	M	·	·	·	c.	·	·	l.f.	·
<i>Prosopis campistre</i> Eng.	M	·	·	·	l.d.	·	·	·	·
<i>P. febrifugum</i> Spach.	M	·	·	·	·	·	·	·	·
<i>Psychotria capensis</i> Vatke	E	·	·	·	·	·	·	·	·
<i>Pediopsis myrtifolia</i> Engl. & Diels.	M	·	·	·	·	·	·	·	·
<i>Peterocarpus angolensis</i> DC.	M	v.l.	·	·	·	·	·	·	·
<i>P. chrysotrichus</i> Taub.	C	·	·	·	·	·	·	·	·
<i>P. polyanthus</i> Harms.	M	·	·	·	l.c.	·	·	·	·
<i>P. rotundifolius</i> (Sond.) Bruce	C	·	·	·	·	·	·	·	·
<i>P. zimmermannii</i> Harms.	R	·	·	·	·	·	·	·	·
<i>Pterolobium laceraens</i> R.Br.	R	·	·	·	·	·	·	·	·
<i>Pygeum africanum</i> Hook. f.	R	·	·	·	·	·	·	·	·
<i>Quisqualis indica</i> L.	M	·	·	·	l.c.	·	·	·	·
<i>Randia kuhniiana</i> F. Hoffm. & K. Schm.	M	·	·	·	·	·	·	·	·
<i>Raphia vinifera</i> Beauv.	R	·	·	·	·	·	·	·	·
<i>Rauvolfia natalensis</i> Sond.	R	·	·	·	·	·	·	·	·
<i>Rhus incana</i> Mill.	·	·	·	·	·	·	·	·	·
<i>R. kweibensis</i> N.E. Br.	M	·	·	·	·	·	·	·	·
<i>R. natalensis</i> Bernh.	Th	·	·	·	l.c.	·	·	·	·
<i>Rothmannia fischeri</i> Bullock	·	·	·	·	·	·	·	f.f.	·
<i>R. taylorii</i> S. Moore	B	·	·	·	c.	·	·	f.f.	·
<i>Rovena annicola</i> B. L. Burtt	Hp	·	·	·	c.	·	·	c.	·
<i>R. fischeri</i> Gürke ex Mildbr.	E	·	·	·	c.	·	·	f.	·
<i>R. lucida</i> L.	P	·	·	·	c.	·	·	l.c.	·
<i>Salvadora persica</i> Garcin.	Th	·	·	·	c.	·	·	f.f.	·
<i>Sapindus busssei</i> Pax.	Th	·	·	·	c.	·	·	f.c.	·
<i>Sarcostemma viminale</i> R.Br.	f.c.	·	·	·	v.c.	·	·	c.	·
<i>Schrebera kiloneura</i> Gilg.	c.	·	·	·	c.	·	·	r.	·
<i>S. mazoensis</i> Sp. Moore	·	·	·	·	f.c.	·	·	c.	·
<i>Sclerocarya birrea</i> Hochst.	c.	·	·	·	f.	·	·	c.	·
<i>S. caffra</i> Sond.	·	·	·	·	f.	·	·	f.	·
<i>Securidaca longipedunculata</i> Friesen.	M	v.r.	·	·	f.c.	·	·	f.	·



Habitat (Shinyanga) (S. Tabora)	Group 1		Group 2		Eastern Province (Kilosa, Morogoro)
	Lake Province	Western Province	Southern Highlands Province (Mbeya)	Nyassaland (Bua River and Domira Bay) (Abercorn)	
<i>Trem guineensis</i> Fic.	R				
<i>Triaenopis speciosa</i> Nied.	R	c.			
<i>Triaenopis cacondensis</i> Hiern.	f.	f.			
<i>T. nyassae</i> Hiern.	Th				
<i>Trichilia emetica</i> Vahl.	E				
<i>Turraea fischeri</i> Gürke	R				
<i>T. holstii</i> Gürke	Th				
<i>T. kaesneri</i> Bak. f.	E				
<i>T. mombassana</i> Hiern.	M				
<i>T. randii</i> Bak. f.	M				
<i>Uapaca homblei</i> De Wild.	M				
<i>U. kirkiana</i> Mull. & Arg.	P				
<i>U. nitida</i> Mull. & Arg.	M				
<i>Ureia fischeri</i> Engl.	Th				
<i>Vangueria edulis</i> Vahl.	R	c.			
<i>V. infusa</i> Burch.	Th				
<i>Vangueria lanceifolia</i> (Hiern.) Roobnns	M				
<i>Vellereya splendens</i> Rendle	R				
<i>Vernonia amygdalina</i> Del.	S				
<i>V. colorata</i> Drake	M				
<i>V. exsertiflora</i> Bak.	E				
<i>Vitex amboinensis</i> Gürke	C	r.			
<i>V. capensis</i> Thonn.	Th	f.c.			
<i>V. hildebrandtii</i> Vatke	M	c.			
<i>V. iringensis</i> Gürke	M	c.			
<i>V. keniensis</i> Turrill	Th	c.			
<i>V. milanjensis</i> Britton	M	c.			
<i>V. mombassae</i> Vatke	M	c.			
<i>V. radula</i> Mildbr.	M	c.			
<i>Ximenia americana</i> L.	M	c.			
<i>X. caffra</i> Sond.	M	c.			
<i>Xylopia antunesii</i> Engl. & Diels.	M	c.			
<i>Xylotheeca spinosa</i> Forsk.	Th	r.			
<i>X. stipulata</i> Oliv.	v.r.	c.			
<i>Ziziphus mauritiana</i> Lam.	c.	c.			
<i>Z. mucronata</i> Willd.	c.	c.			

## X. GENERAL DISCUSSION ON DISTRIBUTION

## 1. THE MIOMBO WOODLAND

The table brings out the contrast between the south-westward transect from Shinyanga to Morogoro, with relatively few *Brachystegias*, and the southward transect to Lake Nyasa, which is very deficient in *Commiphoras* and *Acacias*. Northward and eastward of Mwanza, Shinyanga, Singida, Kondoa and Mpwapwa Districts, the *Brachystegias* disappear altogether, giving place to thorn dominating the Serengeti plains and the Masai Steppe, and the south-eastward transect from Shinyanga to Morogoro therefore runs only just inside the edge of the great *Brachystegia* woodlands extending a thousand miles to the south.

Broadly, we may say that on the south-eastward transect to Morogoro the *Brachystegias* are represented chiefly by *B. spicaeformis*, giving place to *B. boehmii* east from Mpwapwa, with *B. microphylla*, *B. bussei* and occasionally *B. utilis* and *B. allenii* on the kopjes and escarpments; and *Isoberlinia globiflora* co-dominates on the lower ground throughout.

On the southward transect as far as Abercorn, the species of *Brachystegia* become more numerous. In Kahama *B. spicaeformis* and *B. boehmii* are very common, with *B. microphylla* and sometimes *B. utilis* on the granite outcrops. Occasional *B. longifolia* and *B. wangermeana* appear, increasing in abundance as we go southward through Tabora towards Mbeya, where in addition *B. floribunda* clothes many of the high ridges and *B. burttii* the stony hills below. *B. utilis* becomes commoner towards Mbeya, but *B. allenii* does not reappear until we reach the Lake Tanganyika coast near Abercorn (Mr Hornby notes its occurrence in the Iringa area), where also *B. taxifolia* is first encountered round the dambo margins, and occasional stands of *B. stipulata* are met with in the valleys. *B. bussei* is frequent on rocky hills in Tabora, and thence continues southward.

Throughout this transect, except on the high ground, *Isoberlinia globiflora* co-dominates with the ubiquitous *Brachystegia spicaeformis*, and about Abercorn *Isoberlinia paniculata* and *I. densiflora* abound in the miombo woodlands on the higher ground. From Abercorn the miombo then continues with little change through Nyasaland.

The southern *Brachystegia* complex is characterized by a wealth of *Monotes*, of which one or two species are found as far north as Tabora; and from the Southern Highlands Province to Abercorn several Uapacas begin to appear. *Syzygium* spp. also increase about rivers and moist places as we pass southward from Tabora into Mbeya.

In the southern miombo complex, the genus *Strychnos* is very common and well represented by five or more tree species, and other characteristic trees are *Afrormosia angolensis*, *Albizia antunesiana*, *Annona chrysophylla*, *Bauhinia petersiana* and *B. thonningii*, *Burkea africana*, *Crossopteryx febrifuga*, *Diospyros*

*mespiformis* on termite mounds, *Hymenocardia mollis*, *Paivaeusa dactylophylla* and *Pseudolachnostylis maprouneaeifolia*. *Diplorrhynchus mossambicensis* is very common in the eastern miombo about Kilosa as well as in the south, but is rare in the Central Province.

Except certain gall-acacias (*Acacia formicarum* and its allies, and *A. seyal*), *A. albida* of the rivers and *A. ulugurensis* and *A. sieberiana* of the hills, trees of this genus penetrate the miombo little except in the Usangu and Rukwa flats of Mbeya; and of the Commiphoras, *C. fischeri* and *C. pilosa* alone are widely spread through the miombo. Both these genera increase greatly in importance and variety as the Lake and Central Provinces are approached.

The Tabora-Kahama type of miombo continues west of Shinyanga into Mwanza District, where it reaches the Lake Victoria coast. Here are found such characteristic Tabora species as *Hexalobus monopetalus*, *Paivaeusa dactylophylla* and *Burkea africana*. On the other hand, *Albizia versicolor*, common in Mwanza and Kahama as well as near Kikori in Kondoa, is not found in Tabora.

West from Tabora, in Kigoma District, *Brachystegia spicaeformis* continues common, but *B. longifolia* dominates, and *Isoberlinia densiflora* is very common. These two Brachystegias also dominate the Iringa highlands to the east, growing as stunted trees about the 5000 ft. contour.

The allied genus *Cryptosepalum*, looking like a dwarf *Brachystegia*, but with pretty masses of pink, white and blue flowers, characterizes the southern and western miombo. These plants abound in the Abercorn area, and extend northwards through Mbeya into south-western Tabora and on to Kigoma District.

## 2. THE THORN SAVANNAH

Thornbush communities, as already stated, occupy very much of the eastern Lake Province, the northern parts of the Central Province and the Northern Province of Tanganyika, dominating the Serengeti plains and the Masai Steppe.

*Acacia tortilis* savannah is very characteristic of these areas, as well as of the Usangu and Rukwa flats in Mbeya, but is largely replaced in the western Serengeti by *A. hebecladoides*, growing with similarly flat-topped habit. In the Central Province, short grassed flats are characteristically dominated by *A. rovumae*, overtopping the smaller *A. mellifera* and *A. kirkii*; in wetter areas these give place to low-tree savannah of *A. stuhlmannii*. As we go southwards and westwards into Tabora, these species gradually drop out, but *A. rovumae* continues to dominate narrow interzone strips occurring here and there between the miombo and the seasonal swamp. *A. rovumae* does not extend into Rhodesia.

Baobabs (*Adansonia digitata*) are common in the thorn country but are absent from Tabora District except the north-east corner, and do not reappear until we reach the plains bordering Lake Nyasa.

The distribution of the gall-acacias is of particular interest. The common species of Masailand are the red-barked *Acacia formicarum* and the white-galled variety *fistula* of the larger *A. seyal*. They extend south-westwards through Manyoni into parts of Kahama, Tabora and Mbeya—unless the form occurring in Mbeya should prove to be a different though closely related species.

In Kahama and parts of Tabora and Kigoma, *A. burttii* appears, often growing together with *A. formicarum* at the boundaries of their ranges. A new species of gall-acacia with a very large leaf overlaps *A. burttii* in Tabora, and thence continues across the Ugala towards the Rungwa river. In Kigoma this gall-acacia is replaced by another new species of similar appearance but with larger flowers and fruits.

The Wembere gall-acacia is *A. malacocephala*, which penetrates up the Manyonga basin into the Lake Province and occurs locally in south-western Mbulu District also, above the Rift escarpment opposite Hanang.

In the Lake Province *A. drepanolobium* and *A. seyal* are found almost throughout, and the former appears also in parts of the Central Province, notably about Sambala and Usandawe in Kondoa. It extends just south of the Manyonga river in Kahama District.

Gall-acacias are absent from the Abercorn area, but in Nyasaland we find the southern species *A. natalitia* (Phot. 30). *A. zanzibarica* is a purely coastal form in Tanganyika Territory.

Of other important Acacias without galls, *A. nigrescens* dominates very great alluvial flats about Kilosa in the valley of the Wami river; and *A. holstii* is widespread on stony hills, particularly the banded ironstone hills of the Lake Province.

### 3. THE DECIDUOUS THICKETS

The most interesting type is the Itigi thicket of Central Tanganyika, and the characteristic plants (which vary from place to place) are *Baphia massaiensis* and *B. burttii*, *Bussea massaiensis*, *Burttia prunoides*, *Pseudoprosopis fischeri*, *Combretum trothae*, *Grewia burttii*, *Craibia burttii*, *Haplocoelum foliosum*, *Tricalysia cacondensis*, *Justicia salvioides* and *Indigofera subcorymbosa*.

The heart of the thicket is in Manyoni District about the Central Railway, but it extends in all directions. In north-eastern Tabora the thicket apparently lacks *Burttia*, *Bussea* and *Pseudoprosopis*. Itigi thicket is found in western Shinyanga, and *Burttia* occurs also on hills in Shinyanga overlooking the Manyonga river. *Tricalysia* is widespread in Shinyanga, but confined to termite mounds in most of Tabora District.

North and east from Manyoni the Itigi thicket extends far into Singida, and Usandawe in Kondoa. It is found in Dodoma District, but in Mpwapwa the only representatives are *Justicia salvioides*, *Tricalysia cacondensis* and *Indigofera subcorymbosa*, together with the grass *Anthepehra burttii* which invades paths and open spaces in it. From Dodoma, the thicket extends southwards into Iringa.

Surprisingly, the Itigi type of thicket reappears in rocky gorges near Abercorn, where *Baphia*, *Burttia*, *Pseudoprosopis*, *Craibia*, *Haplocoelum* and *Indigofera subcorymbosa* were noted. *Combretum trothae* however was replaced by *C. celastroides*.

A quite different type is the *Commiphora-Cordyla* thicket of Mpwapwa and the Lukosi valley in Usagara to the south. The characteristic species are *Commiphora hornbyi*, *C. merkeri*, *Cordyla africana* and *Caesalpinia trothae*, and the mass of the thicket is composed of *Acalypha*, *Grewia*, *Croton*, *Disperma* and *Acacia pennata*.

In the Lake Province and part of the Central Province other kinds of thicket are found. In Musoma District the commonest thicket elements are *Harrisonia abyssinica*, *Grewia bicolor*, *Rhus glaucescens* and *Acacia pennata*, with a fresh-green, bayonet like *Sansevieria* growing below. In Shinyanga, the primaeva hill thickets are characterized by the trees *Commiphora emini*, *Ficus sonderi*, *Vitex keniensis*, *Maba abyssinica*, *Teclea nobilis* and *Combretum molle*. The mass of the thicket is composed of *Acalypha*, *Acacia pennata*, *Dalbergia ochracea*, *Strychnos matopensis*, *Urera fischeri* and *Justicia salvioides*. On the lower ground, *Abrus schimperi*, *Markhamia acuminata*, *Grewia platyclada*, *Dalbergia ochracea*, *Hippocratea loesneriana* and *Acacia pennata* are particularly abundant in the thickets, which are overtopped by *Commiphora ugogensis*, *Delonix elata*, *Entandrophragma bussei*, *Sclerocarya birrea* var. *multifoliolata* and *Strychnos heterodoxa*.

In Abercorn, the cliffs near the lakeshore are often covered with thicket characterized by *Abrus praecatorius*, *Cassytha filiformis*, *Vitex radula* and *Bauhinia petersiana*, with other species more widespread.

#### 4. THE COMBRETUM COMMUNITIES

In the Lake Province the rising ground is usually dominated by *Ostryoderris stuhlmannii*, with much *Terminalia sericea* and abundant *Combretum zeyheri*, and a good growth of grass. Rather similar country is found in the Eastern Province and in Nyasaland. In the Central Province this type is encountered chiefly as an interzone between Itigi thicket and the hard pan country below, or between the miombo and the hard pan.

In Kigoma, Kahama, Tabora and parts of Nyasaland, flat-bottomed drainage valleys are clothed with *Combretum ghasalense*, with early flushing, fresh green leaves. In Musoma District on the other hand, and locally in other parts of the Lake Province, this species dominates on banded ironstone hills.

A different kind of *Combretum* country is common in Tabora and local in Mwanza. *Combretum ghasalense* and *Crossopteryx febrifuga* are the characteristic small trees. There are numerous termite mounds clothed with thicket and topped by large trees, and away from the termite mounds the commonest large species are *Afromosia angolensis* and *Pterocarpus chrysotricha*.

### 5. HIGHLAND GRASSLAND

This type occurs between the upland *Brachystegia* woods and the evergreen forest around 7000 ft. The common trees are *Protea* spp., *Erythrina abyssinica*, *Acacia sieberiana* and *A. abyssinica*, *Faurea speciosa*, *Dombeya quinqueseta* and *Uapaca* spp. in the south. In the Southern Highlands *Parinari curatellae-folia* is very common.

### 6. EVERGREEN FOREST AND RIVERINE COMMUNITIES

As editor, I can give this section only sketchy treatment, as I am not familiar with evergreen forest types; and also Burtt's duties, taking him mainly into the savannah, did not allow him to leave very complete records of the evergreen forest.

*Podocarpus* forest survives as relict patches on the high hills north of Kondoa, on Hanang, and on the Uluguru mountains of Morogoro.

At Mpwapwa *Podocarpus* is apparently absent, but the usually associated species *Calodendrum capense*, *Apodytes dimidiata*, *Phoenix reclinata* and *Albizia gummifera* are common.

The peculiar swamp forests of Abercorn are dominated by *Albizia glabrescens*, *Syzygium*, *Chrysophyllum*, *Sorindeia*, *Ficus* and *Elaeis*.

Evergreen riverine forest is found in Mwanza, Mpwapwa, the Eastern Province, Abercorn and Nyasaland. In Abercorn, *Syzygium cordatum* and *S. guineense*, *Berlinia craibiana* and *Gardenia imperialis* are common. Elsewhere, species of *Albizia* and *Ficus* predominate, and *Trichilia emetica*, *Parkia filicoidea* and *Combretum schumannii* are widespread.

In regions of lower rainfall or lower altitude deciduous riverine forest appears. In the Lake and Central Provinces, common large trees are *Ficus sycomorus*, *Piptadenia hildebrandtii*, *Albizia brachycalyx* and *Acacia campylacantha*. In Parts of Musoma District, about the Wembere, in Mpwapwa, Usagara, Mbeya and Nyasaland, the deciduous riverine forests are usually dominated by *A. albida*, which is locally common near Abercorn. *A. xanthophloea* forms riverine or lakeshore forests around Lake Manyara, on the Bubu river near Kondoa, and on the lake at Babati, and about Lake Rukwa in Mbeya.

The few large rivers of Tabora District are distinguished by the dominance of *Syzygium guineense*, and by the absence of *Acacia campylacantha*, *A. albida* and *Piptadenia*. Big *Diospyros mespiliformis* are characteristic, with *Garcinia livingstonei*, the widespread *Acacia sieberiana*, and thickets of *Canthium gueinzii* and *Antidesma venosum*.

Palm savannah is often associated with rivers, their flood plains, and the swamps into which some of them debouch. *Borassus aethiopum* is common in southern Singida and Manyoni, on rivers draining to the Wembere Steppe, but not east of the Rift Wall. It is widespread in Kahama and Tabora.

especially in old cultivation and on the flood plain of the Ugala river; and it occurs in river valleys in the Abercorn District.

The Bubu and Mponde rivers lose themselves below the Kilimatinde escarpment in a plain dominated by *Hyphaene crinata*, which occurs also along the courses of these rivers. On the Ugala river flats, *Hyphaene* is fairly common among the more abundant *Borassus* palms, and it dominates the flats around Lake Rukwa, and some of the Nyasaland dambos.

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# THE EXCHANGE OF DISSOLVED SUBSTANCES BETWEEN MUD AND WATER IN LAKES<sup>1</sup>

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## §§ III AND IV, SUMMARY AND REFERENCES

### III. THE RELATION OF SEASONAL VARIATIONS IN REDOX CONDITIONS IN THE MUD TO THE DISTRIBUTION OF DISSOLVED SUBSTANCES IN THE WATER OF ESTHWAITE WATER AND WINDERMERE

THE interdependence, demonstrated in § II, between changes in concentration of dissolved substances in the water and redox conditions in the mud, and also the similarity of these changes to those observed in the hypolimnion of Esthwaite Water and other lakes (§ I), suggests that redox conditions in the mud also control the distribution of dissolved substances in natural lake systems. The work described in this section was designed to obtain information on this point. A chemical survey on Esthwaite Water, similar to that carried out during 1939, was repeated during 1940, and at the same time the distribution of redox potential and other variables was investigated in undisturbed short cores of the surface mud and overlying water, obtained with sampling apparatus designed for this purpose. Esthwaite Water and lakes of similar type (e.g. Blelham Tarn) were chosen for detailed study, because the range of variation of redox conditions and distribution of dissolved substances is sufficiently wide to allow significant correlations to be recognized. It is, however, of equal importance to attempt to discover the reasons for the small seasonal amplitude of physical-chemical variation observed in lakes of oligotrophic type. Accordingly, the investigation of seasonal changes in the mud and water, by methods described in this section, has been extended to lakes in which de-oxygenation of the hypolimnion, and the changes associated with it, does not occur. Results of investigation on Windermere (northern basin)—a representative of this type of lake—have been selected here for comparison with Esthwaite Water. A chemical survey extending over the years 1936–40 has been carried out on Windermere in connexion with bacteriological and algological investigations. The full results of this survey will be published later. Some data for temperature, dissolved oxygen and distribution of bacteria have already been published by Taylor (1940). In addition, P. M. Jenkin (unpublished results) studied the distribution of temperature and dissolved oxygen in Windermere, north and south basins, during 1931–2.

<sup>1</sup> Continued from the previous number of this *Journal* (Aug. 1941).

## SAMPLING TECHNIQUE

*Jenkin surface mud sampler.* The first essential for this work was a method by means of which a sample of the surface mud and the water immediately overlying it could be obtained for laboratory examination with the least possible disturbance of stratification of physical-chemical variables. This problem has been satisfactorily solved by Mr B. M. Jenkin, whose assistance in

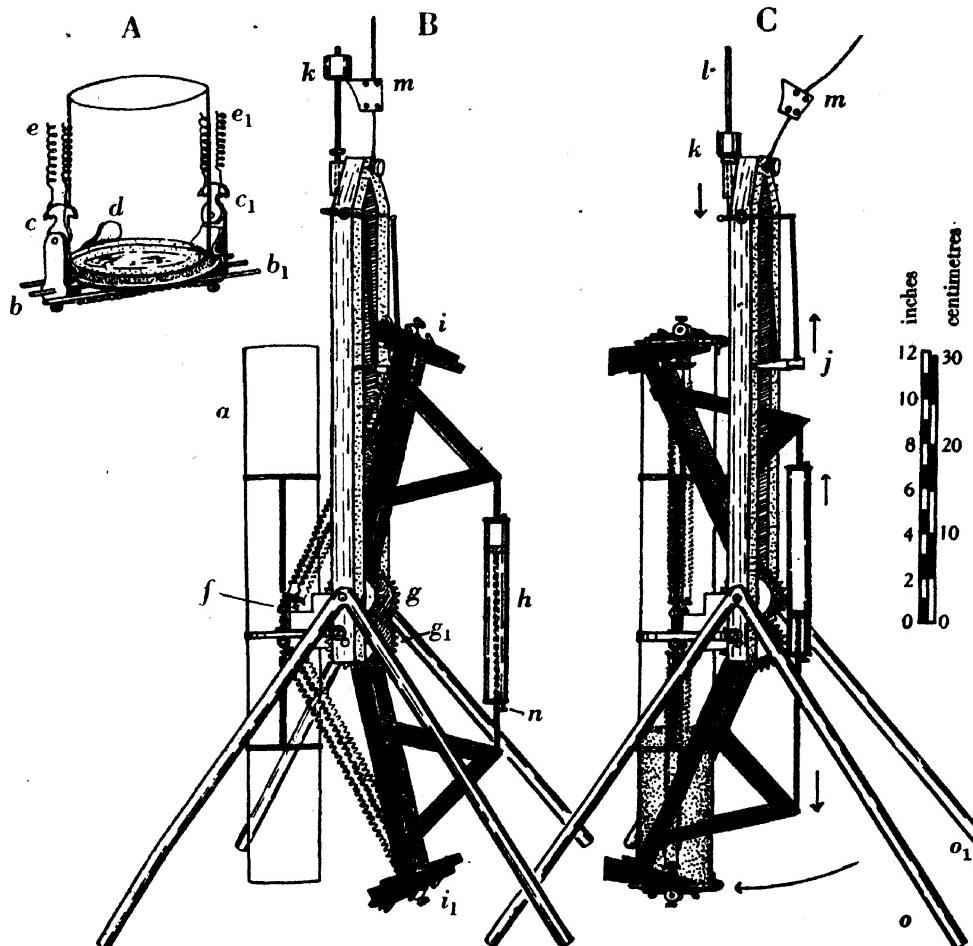


Fig. 22. Diagram of surface mud sampling apparatus. A. Details of lid. B. Open position. C. Closed position, with sample. For other letters see text.

this matter I gratefully acknowledge. The first experimental model of the 'surface mud sampler', which he designed and constructed and which is shown in Fig. 22, worked satisfactorily and was employed throughout this investigation. It is of use in all cases where an undisturbed sample of the surface mud and water in contact with it is required for chemical, faunistic or other investigation. The apparatus will be described more fully elsewhere. Its working principles are outlined here.

The sample is taken in a glass tube (Fig. 22, *a*), 2 ft. long and 3 in. diameter. Each end is ground flat and provided with a lid (Fig. 22 A) which consists of a glass disk over which a wide rubber band is slipped to give the lid a facing of rubber. This lid forms a watertight seal with the end of the tube, and is backed by a metal disk, which carries cross-bars (*b*, *b*<sub>1</sub>) projecting beyond the rim of the lid, attachments (*c*, *c*<sub>1</sub>) for springs, and a metal heel (*d*), the purpose of which is explained later. Each lid is held tightly pressed against the end of the tube by a pair of steel springs (*e*, *e*<sub>1</sub>) on either side, stretching between the lid attachments (*c*, *c*<sub>1</sub>) and attachments (*f*) at the middle of the tube on a strip-metal harness, in which the tube is enclosed (Fig. 22 B). The tube with its lids and attachments forms a container in which the sample may be transported without loss.

The tube is mounted in a framework to which four legs (*o*, *o*<sub>1</sub>) are rigidly fixed in such a manner that the framework and tube are supported vertically during manipulation and transport. This framework carries an upper and a lower pair of arms, pivoted at (*g*, *g*<sub>1</sub>), each pair being connected together by cross-struts. In addition, the upper pair is geared to the lower pair by gear wheels at (*g*, *g*<sub>1</sub>); the two pairs are also linked by a dashpot (*h*) (consisting of the barrel and piston of a cycle pump). At its distal extremity each arm carries a plate (*i*, *i*<sub>1</sub>) arranged in such a manner that, when the arms are rotated in the direction away from the tube (clockwise as Fig. 22) the plates first make contact with the cross-bars (*b*, *b*<sub>1</sub>) on either side of the lids. As described above, the arms are geared to move together, and further rotation of the arms in the same direction lifts the lids away from the tube, against the tension of the springs to the 'open' position (Fig. 22 B). The arms are held in this position by a trip-catch (*j*).

In this position, with the sampling tube completely open, the apparatus is lowered to the mud surface. As long as the winch cable remains taut, a weight (*k*), which slides on a vertical rod (*l*), is held in a raised position by a metal bracket (*m*) attached to the winch cable. The framework legs are so weighted with lead wrappings that, when the apparatus reaches the mud surface, its momentum carries the sampling tube to about one-quarter of its length into the soft mud. The winch cable goes slack and the weight (*k*) falls and releases the trip-catch (*j*). The tension of the springs (*e*, *e*<sub>1</sub>) then pulls the arms carrying the lids counter-clockwise, thus closing the tube (Fig. 22 C, arrows indicate direction of motion). To avoid disturbance of the sample, the dashpot, which is at this stage full of water, ensures that this closing operation shall proceed slowly. The rate may be regulated by a valve (*n*) on the outlet of the dashpot barrel. The springs are sufficiently powerful to cause the bottom lid to slice through the soft surface mud and close the bottom of the tube. The heel (*d*, Fig. 22 A) prevents the lids from passing beyond the ends of the tube.\* Operated by a separate pair of springs (not shown in figure), the arms pass on and leave the lids to close down on the ends of the tube and to keep it

closed by the tension of their springs. The plates ( $i_1$ ) on the bottom arms are so arranged that the bottom lid closes slightly before the top one. The apparatus is then hauled up and the tube and its contents may be removed from the framework.

Samples obtained in this manner appeared to be undisturbed, except for a little smearing of surface mud to lower levels at the side of the tube. Stratification of colour and texture was preserved, the surface flocculent layer including insect tubes and casts appeared undisturbed and the water was clear. Also, the preservation of the marked vertical stratification observed just above and below the mud surface is evidence of the undisturbed condition of the sample.

Immediately after sampling, i.e. in the boat, the top lid was removed and water from just above the mud surface was siphoned through a rubber tube into 100 c.c. bottles for  $O_2$ ,  $CO_2$  and redox potential determinations. In all three cases the same precautions were observed as in sampling for dissolved oxygen determination. In order to obtain the volume of sample necessary for all determinations from the lower part of the tube only, the three 100 c.c. bottles, after having been carefully washed on the outside and inside, were placed as shown in Fig. 23 in a clean glass funnel and held together by a rubber band. The overflow from flushing the bottles, to expel air and water which had been in contact with it, was collected in the funnel, passed into a larger sampling bottle and used for other determinations. Another sample of mud and overlying water was then taken, with the apparatus already described, and transported to the laboratory. Samples from Esthwaite Water and Windermere were usually examined within 30 min. of sampling.

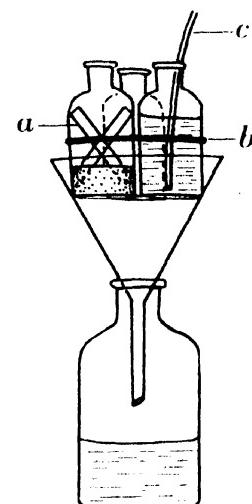


Fig. 23. Arrangement for sampling water from just above the mud surface.  
a,  $CO_2$ -bottle with glass baffle strips supported in paraffin wax; b, rubber band; c, siphon from sampling tube.

#### OTHER METHODS

##### *Redox potential above and below the mud surface*

Bright platinum electrodes, described in § II (Fig. 16), were lowered into the mud core (Fig. 24) as soon as it had arrived in the laboratory, and the potentials at small depth intervals above and below the mud surface were measured 2 hr. after this. During this period the water at the top of the sampling tube had been exposed to air. Study of the rate of change of distri-

bution of redox potential and conductivity in samples examined at varying time intervals after sampling, showed that conditions in the mud and in the water a centimetre or so above it, after transport and the 2 hr. interval necessary for the electrode potentials to attain a relatively steady value, represented field conditions sufficiently closely for the purposes of this investigation. This conclusion is consistent with the slow rate of diffusion of solutes in the mud and with the slow rate of oxidation or reduction of the mud surface (cf. Fig. 28 and later discussion). The above measuring technique, however, caused considerable change in the distribution of redox potential and conductivity at higher levels in the water. Consequently, only those samples siphoned off in the field were relied upon to supply information on conditions in the water just over the mud. The values indicated for water above the mud surface in Figs. 28, 30, 32 and 33 were obtained from these samples, using methods described in § I.

#### *Electrical conductivity above and below the mud surface*

Before inserting the redox-potential electrodes, the conductivity at each centimetre level in the mud core was determined with the apparatus and electrodes described earlier (Fig. 16). It was arranged that the electrodes should penetrate the core at points removed from the region in which the redox electrodes were subsequently inserted. Usually the mean of two or three vertical series was taken. Measurements at the same level normally showed close agreement. The conductivity values entered in Figs. 30, 33, 34, 35 and 45 represent the apparent conductivity of the mud, assuming that the temperature of the whole core is the same as at the surface. This value is not necessarily the same as the conductivity of the interstitial water in the mud, as the masking effect of the mud solids on the electrodes has not been considered. However, the results are reproducible, comparable and adequate for the study of seasonal and regional variation.

#### *pH of mud core*

After the measurements of redox potential and removal of the electrodes, the water was siphoned out of the sampling tube as completely as possible and the mud core was pushed up to the top of the tube by means of a piston. This operation apparently caused little disturbance of the core except at the sides. The core was then sliced with a thin metal plate into approximately centimetre layers, or other convenient thicknesses, as it emerged from the tube. pH estimation was carried out with a quinhydrone electrode. The procedure and the calculation of  $E$ , values for different mud levels was described in § II.

#### *Estimation of dissolved substances in the water*

The methods and extent of the chemical survey in the water, carried out at the same time as the investigation of the mud, in Esthwaite Water were closely similar to those described for 1939 in § I. Many of the results obtained

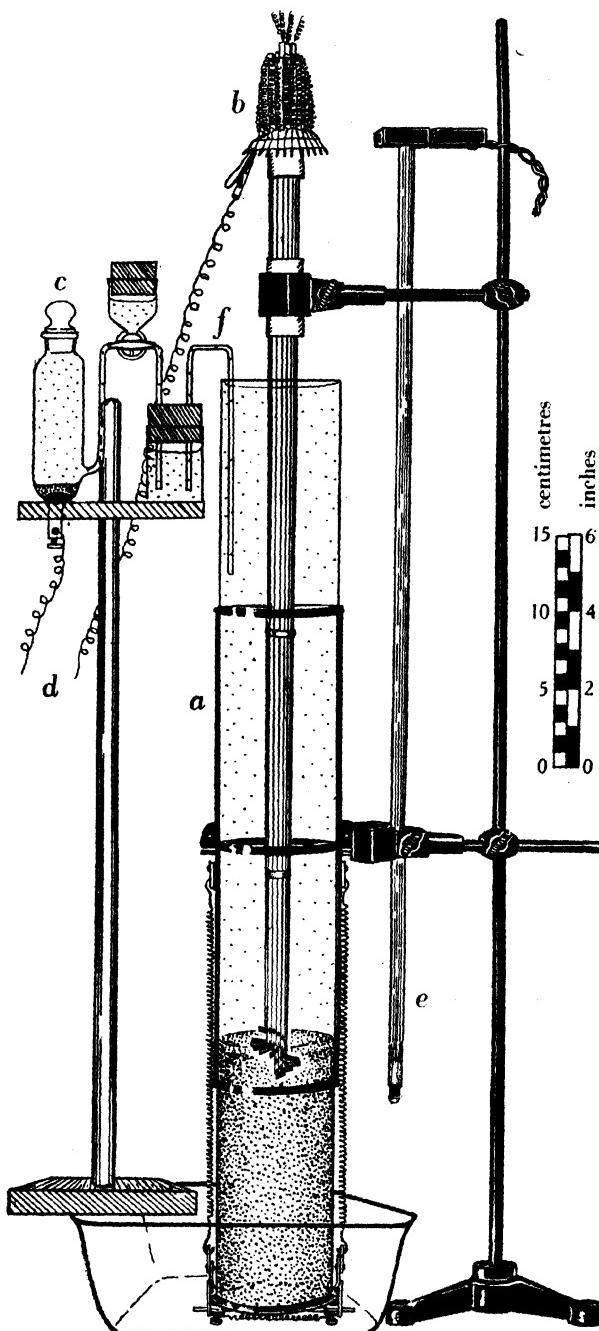


Fig. 24. Arrangement for the investigation of the distribution of redox potential and electrical conductivity in surface mud cores. *a*, sampling tube; *b*, redox electrodes; *c*, calomel electrode; *d*, leads to potentiometer; *e*, conductivity electrodes; *f*, KCl-agar bridge.

in 1939 were confirmed in 1940. Only a selection of these latter results, sufficient to indicate the course of thermal and chemical stratification, will be included here. Manganese, and occasionally chloride, was added to the routine determinations during 1940:  $\text{CO}_2$  was estimated by a modification of the method described in § II. 100 c.c. bottles were fitted with glass baffle strips supported in paraffin wax, as shown in Fig. 23. Samples were collected in these with the same precautions used in the collection of oxygen samples. Titration was carried out in the sampling bottle, by the method described in § II, after 5 c.c. had been removed for colorimetric pH determination. Alsterberg's modification of Winkler's method (cf. Ohle, 1936b) was employed for dissolved oxygen determination in all cases where the presence of reducing substances was suspected. 'Biochemical oxygen demand' was estimated by a standard method (Amer. Publ. Hlth Ass. 1936) on the same sample in which redox potential had previously been measured, care having been taken to exclude air during the measurement. Oxygen introduced with the electrodes was neglected.

Similar series of determinations were carried out at various depths in Blelham Tarn, Windermere north and south basins and other lakes, at the same time as an investigation of the mud surface by the methods described above.

## RESULTS

### A. Esthwaite Water, May 1940–March 1941

*Weather and thermal stratification.* Except for one storm during May, calm fine weather initiated thermal stratification at an earlier date than in 1939. The hypolimnion was also much colder and less stratified than during 1939 (cf. Figs. 3, 26). Further correlations between weather and stratification may be observed by comparison of Figs. 25 and 26.

*Distribution of (a) dissolved oxygen, (b) redox conditions near the mud surface and (c) concentration of solutes in the water just above the mud* (Figs. 27–29). Soon after thermal stratification had become established and the oxygen concentration just above the mud had begun to fall (Fig. 27), the oxidized surface mud layer, the bottom of which may be taken (cf. § II) approximately as the isovolt  $E_7=0.20$  V. (thickened line in Fig. 28), was reduced to a thin layer at the mud surface, finally disappearing on 12 June. After this date the concentrations of iron, carbon dioxide and colour in the water began to rise more rapidly; dissolved oxygen concentration and transparency began to fall more rapidly, and manganese appeared (Fig. 29). However, probably as a result of rough weather and relatively high turbulence in the hypolimnion at the end of June, the isovolt  $E_7=0.20$  V. did not rise into the water until nearly a month after it had appeared at the mud surface. By this time (July) the oxygen concentration above the mud had fallen to just below 1.0 mg./l., and ferrous iron was detected in the water. During the weeks preceding this, the

concentrations of iron, ammonia, colour, silicate, conductivity and alkalinity had shown marked increases, while the concentrations of nitrate and sulphate

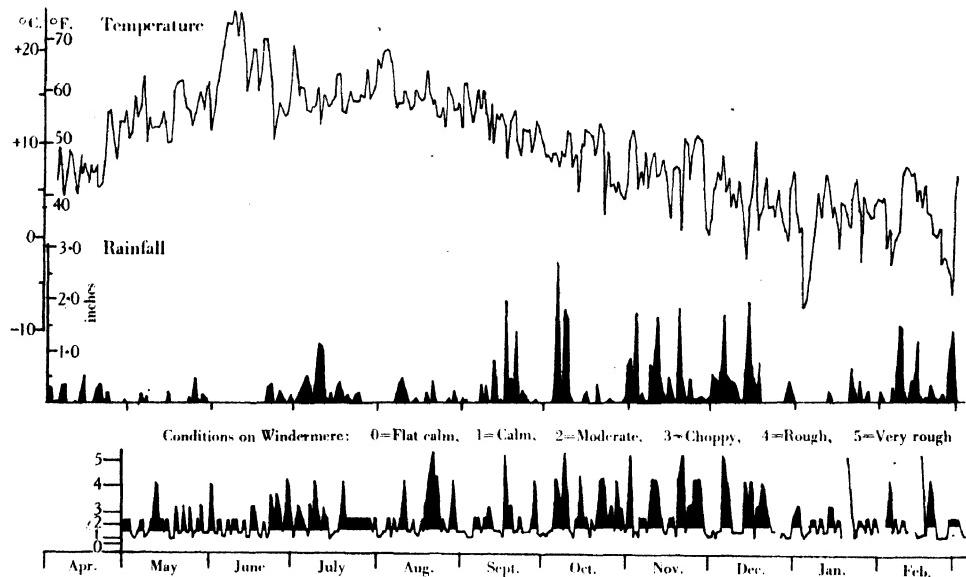


Fig. 25. Meteorological records, 1940-1. Air temperature (9 a.m. Ambleside), rainfall (daily totals Ambleside) and observations on Windermere (estimate of mean daily condition).

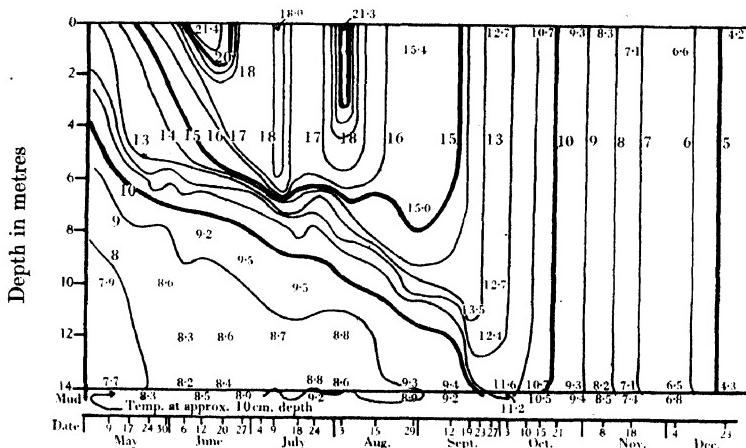


Fig. 26. Esthwaite Water, 1940. Depth-time diagram of the distribution of temperature ( $^{\circ}\text{C}$ ) in water and mud surface (approx. 10 cm. below the surface).

had decreased (Fig. 29). Transparency had also considerably decreased owing to the presence of cloudiness resulting from the precipitation of ferric hydroxide produced by oxidation of ferrous iron at the mud surface.

Apart from the sudden increases in concentration of ferrous iron, phosphate and reducing substances (oxygen demand), which occurred during subsequent weeks, the *initial* rate of increase, at the beginning of July, in concentration

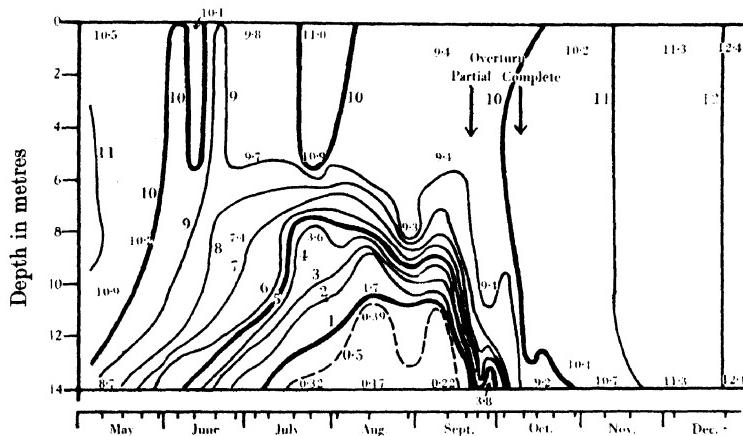


Fig. 27. Esthwaite Water, 1940. Depth-time diagram of the distribution of dissolved oxygen (mg./l., using Alsterberg's modification of Winkler's method). Note. Sampling dates in this and subsequent figures as in Fig. 26.

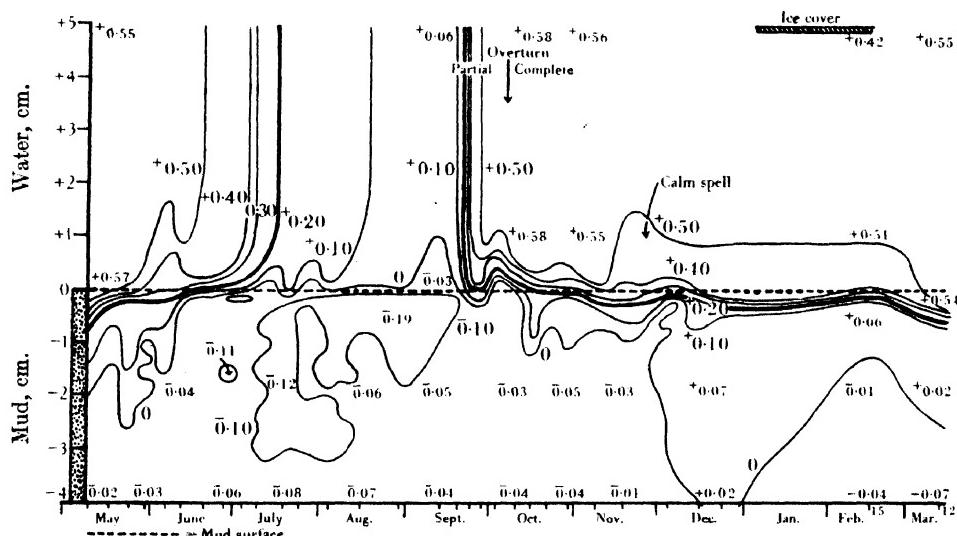


Fig. 28. Esthwaite Water, 1940. Depth-time diagram of the distribution of redox potential above and below the mud surface, 14 m. ( $E_7$  in volts).

of most solutes (ammonia, conductivity, alkalinity, silicate, manganese and total iron) and colour and turbidity, was not maintained during the later summer. During this period a slower increase, with some fluctuations, occurred in most cases until the overturn (Fig. 29).

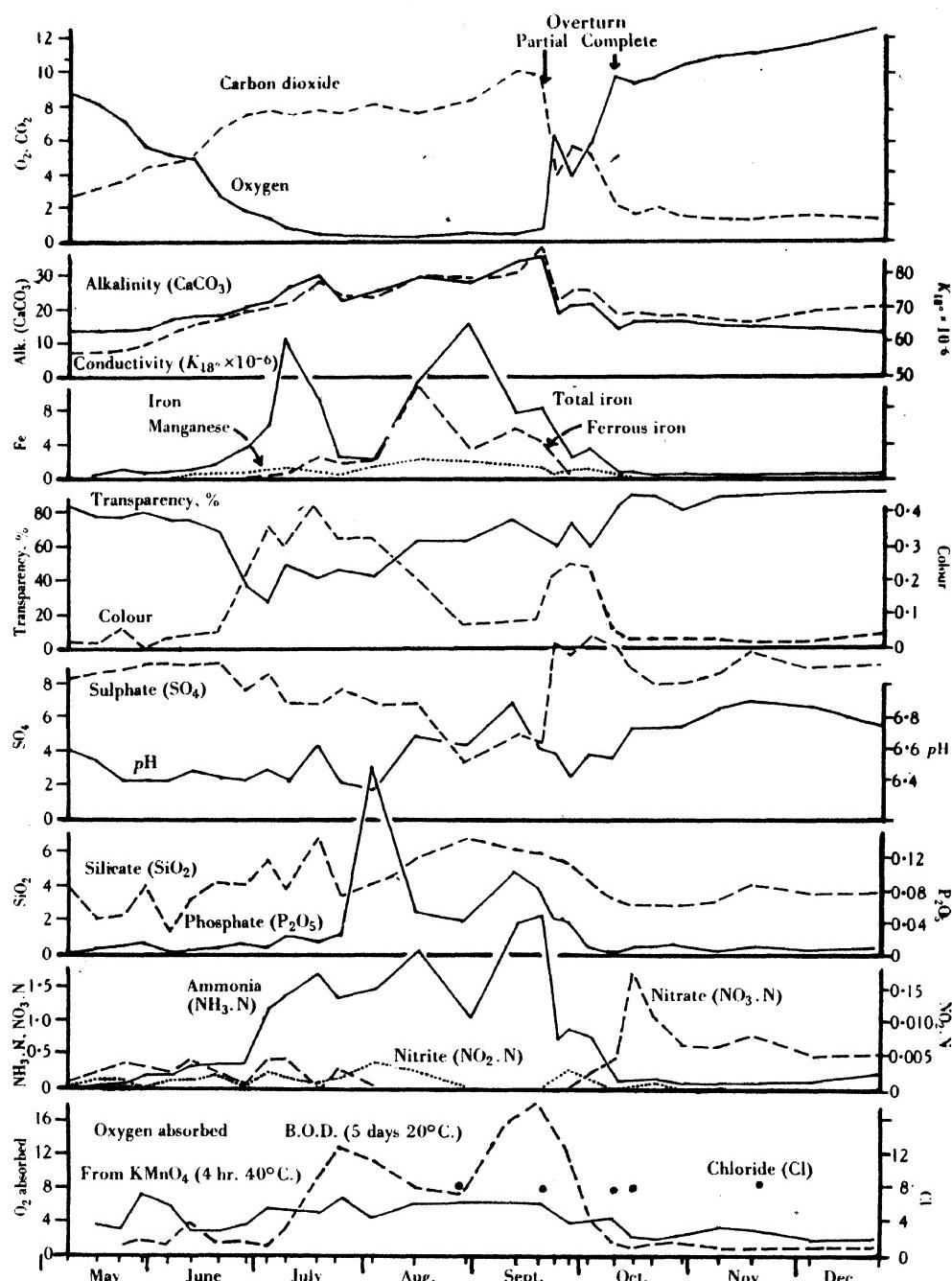


Fig. 29. Esthwaite Water, 1940. Concentrations of dissolved substances in water just over the mud surface, 14 m. (mg./l.).

Changes in total content of phosphate and silicate in the whole water column are shown in Fig. 12, § I.

The same series of changes observed at the overturn in Esthwaite Water 1939 were repeated during 1940. A partial overturn occurred as the result of a gale on 17 September, followed by a calm spell (see Figs. 25–27). Circulation was not complete until the stormy weather after 5 October. The effect of these weather oscillations on the redox potential and concentration of solutes at the mud surface may be seen in Figs. 28 and 29. A change in the ratio of alkalinity to conductivity was observed after the overturn (1940), indicating, as in 1939, the adsorptive removal of bases from the water by the oxidized mud surface. The fall in ammonia concentration at the partial overturn was followed by a nitrite maximum, itself followed by a comparatively high nitrate maximum 3 weeks later. Ferrous iron disappeared at the partial overturn, but manganese did not disappear until a fortnight later. A fall in transparency at the end of September was associated with the oxidation of ferrous iron. Phosphate concentration fell to minimal values after the overturn, and the concentrations of silicate, colour and reducing substances (oxygen demand) also decreased. Sulphate, which had only been reduced to half its original spring concentration, approximately doubled in concentration after the overturn.

*Redox conditions after the overturn* (Fig. 28). It was some weeks after the overturn before the oxidized layer became fully developed at the mud surface, and the isovolt  $E_7=0.20$  V. remained at a relatively steady 'winter' level below the mud surface, comparable with that observed during May. The thickness of the oxidized layer was subject to considerable fluctuations. During a calm spell in December it consisted only of a surface scum containing ferric hydroxide, and it was again almost destroyed during stagnation under ice from 3 January to 15 February 1941. Samples were taken on the latter date while the ice was still breaking up and before circulation of the lower water had begun. The last sample on 12 March completed the investigation of an annual cycle, as it may be assumed that the oxidized layer remained at approximately the same thickness from March until thermal stratification and de-oxygenation recommenced in the spring.

*Conductivity of the mud* (Fig. 30) increased at all the levels investigated after thermal stratification had been established and rose to a maximum at the mud surface on 24 July. Possible reasons for this considerable increase and for the subsequent fall in the conductivity of surface layers will be discussed later. Some considerable oscillations in conductivity values were observed at the period of the overturn, followed by a fall in conductivity at all levels to low values comparable with those found at the beginning of May. Another marked rise in conductivity at all levels was observed after the period of stagnation under ice. This was followed by a decrease in conductivity similar to that observed after the overturn.

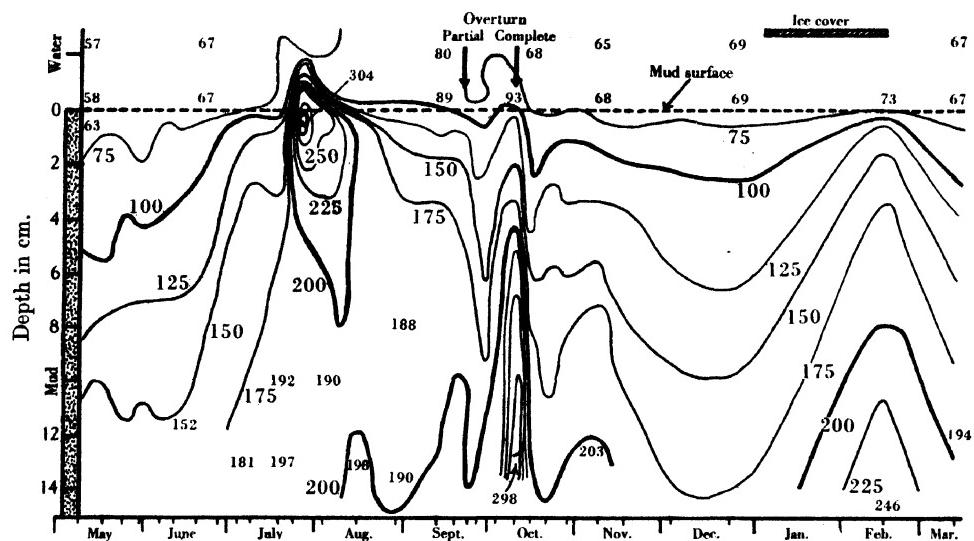


Fig. 30. Esthwaite Water, 1940-1. Depth-time diagram of the distribution of electrical conductivity above and below the mud surface, 14 m. ( $K_{18^\circ} \times 10^{-6}$ ).

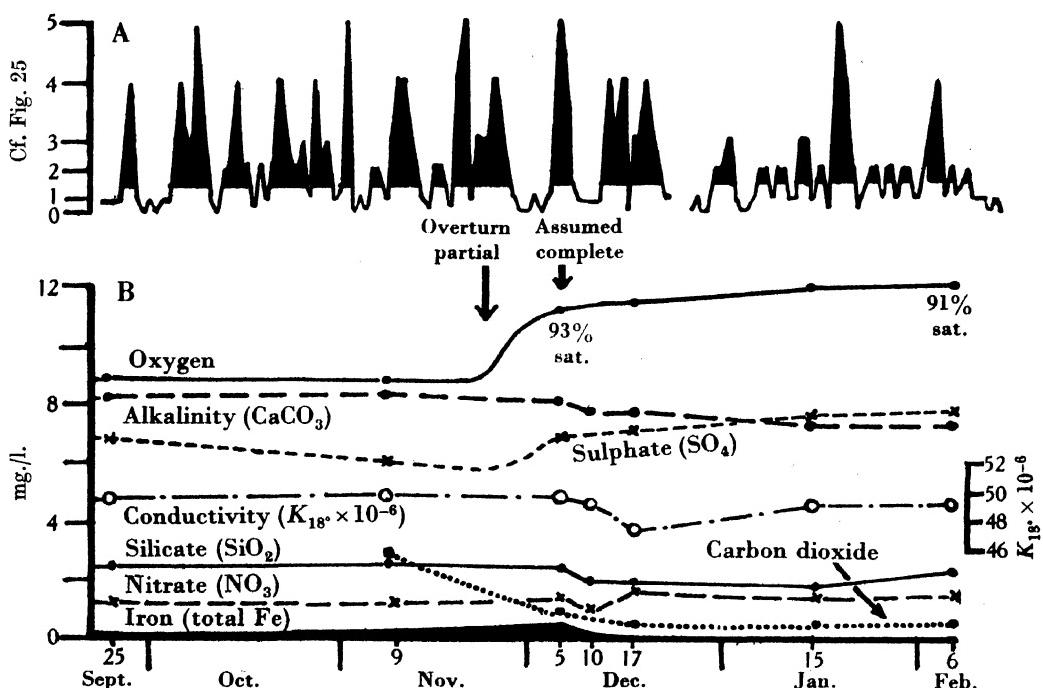


Fig. 31. Windermere, North Basin, 1940-1. A. Weather observations (estimate of mean daily condition). B. Concentrations of dissolved substances in water just over the mud surface, 65 m. (mg/l.).

B. Windermere, North Basin (25 September 1940 to 6 February 1941)

Seasonal changes in physical and chemical variables in the surface mud and the water immediately overlying it were investigated, by the same methods employed on Esthwaite Water, at a station (65 m. depth) in the deep region of the North Basin of Windermere, over a period which included  $2\frac{1}{2}$  months before and after the overturn. From Fig. 31, which indicates (a) weather conditions on Windermere and (b) concentrations of some dissolved substances

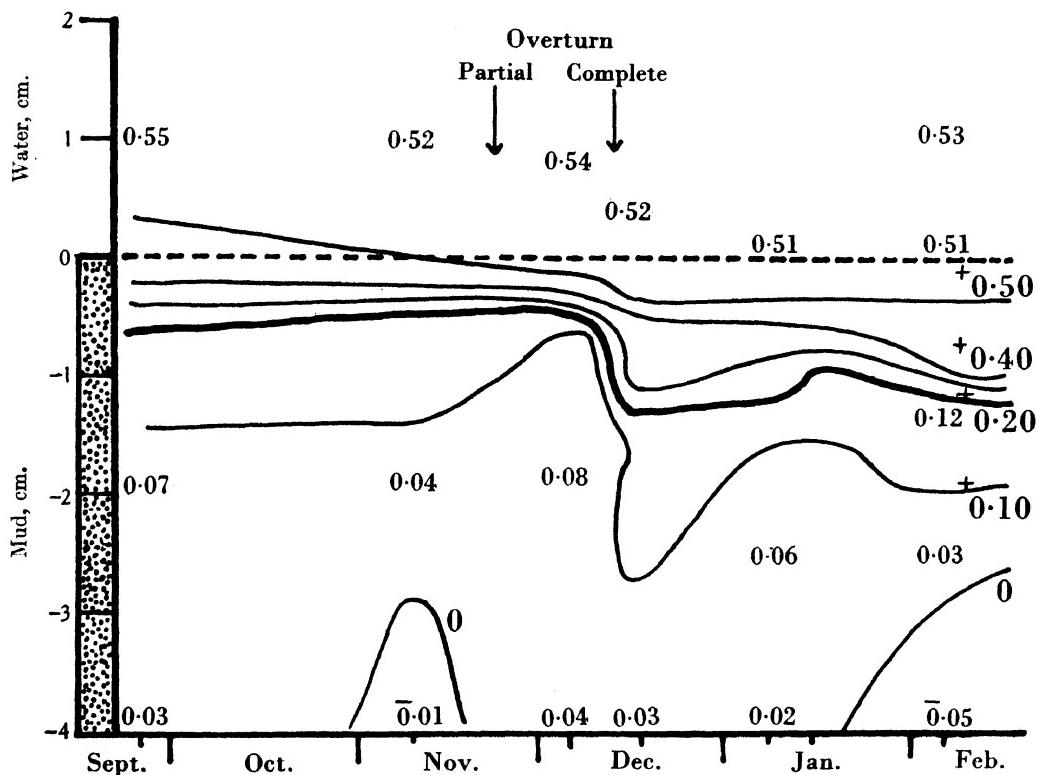


Fig. 32. Windermere, North Basin, 1940-1. Depth-time diagram of the distribution of redox potential above and below the mud surface, 65 m. ( $E_7$  in volts).

in the water siphoned from just over the mud in the sampling tube, it may be assumed that the overturn occurred as a result of a gale on 21 November and was completed by the gale on 5 December.

The oxygen concentration above the mud at the end of thermal stratification was 8.8 mg./l. or 71% saturation at  $6.4^\circ\text{C}$ . The oxidized layer (Fig. 32) was not destroyed during the stagnation period, but it may be assumed that it had become gradually reduced in thickness, for after the overturn its thickness was approximately doubled.

Changes in concentration of dissolved substances in the water above the

mud, which occurred at the overturn, were definite but extremely small compared with those which occurred during the overturn in Esthwaite Water. A fall in the concentration of carbon dioxide and iron, and slight decreases in the concentrations of silicate, alkalinity and conductivity were observed. Calculation shows that the fall in conductivity can be accounted for by the decrease in concentration of substances producing alkalinity. This suggests that the adsorption of bases, observed in Esthwaite Water after the overturn and attributed to adsorption at the mud surface, also occurs in Windermere, although the effect is much less marked in the latter case. During the 2 months after the overturn, alkalinity fell slowly, while the conductivity remained constant. Data from analyses of inflow waters are not available to decide whether this change is due to continued adsorption of bases and liberation of anions other than bicarbonate (note increase in sulphate during the same period), or whether it must be attributed to changes in composition of inflow water. Sulphate and nitrate rose in concentration slightly after the overturn. Ammonia, nitrite and phosphate were only present in traces before and after the overturn. The concentration of oxygen during the period after the overturn represented percentage saturation values of about 92 at the temperatures concerned.

Although the conductivity of the mud core showed some fluctuations (Fig. 33), there was clear evidence of a fall in conductivity in all but the surface layers during the month following the overturn. A rise was noted at the end of January. Further evidence of seasonal change in conductivity in the mud is afforded by the comparison (Figs. 34, 35) of the vertical distribution of conductivity in a number of surface mud cores from the deep region of the North Basin of Windermere before and after the overturn. All the samples were taken at points, fixed by sextant bearings, within the 50 m. contour, i.e. within an area of approximately 1 km.<sup>2</sup> Fig. 34 indicates the degree of local variation which was found, but shows that, in spite of this variation, there is little overlapping between the group of cores taken (A) at the end of summer stagnation (autumn 1939) and (B) at the end of winter circulation (spring 1940). Mean curves for these two groups are presented in Fig. 35. Useful data on the rate of production of ions at different levels in the mud may be obtained by mathematical analysis of such curves (see § IV).

#### DISCUSSION

The occurrence of relatively slight changes similar to those just described for Windermere, North Basin, was confirmed by a similar study in the South Basin of Windermere over the same period. Investigation of single samples taken on other lakes (Thirlmere, Crummock Water, Ennerdale, Derwentwater) at different times of the year, suggests that similar changes occur in all lakes where de-oxygenation of the hypolimnion does not take place. On the other

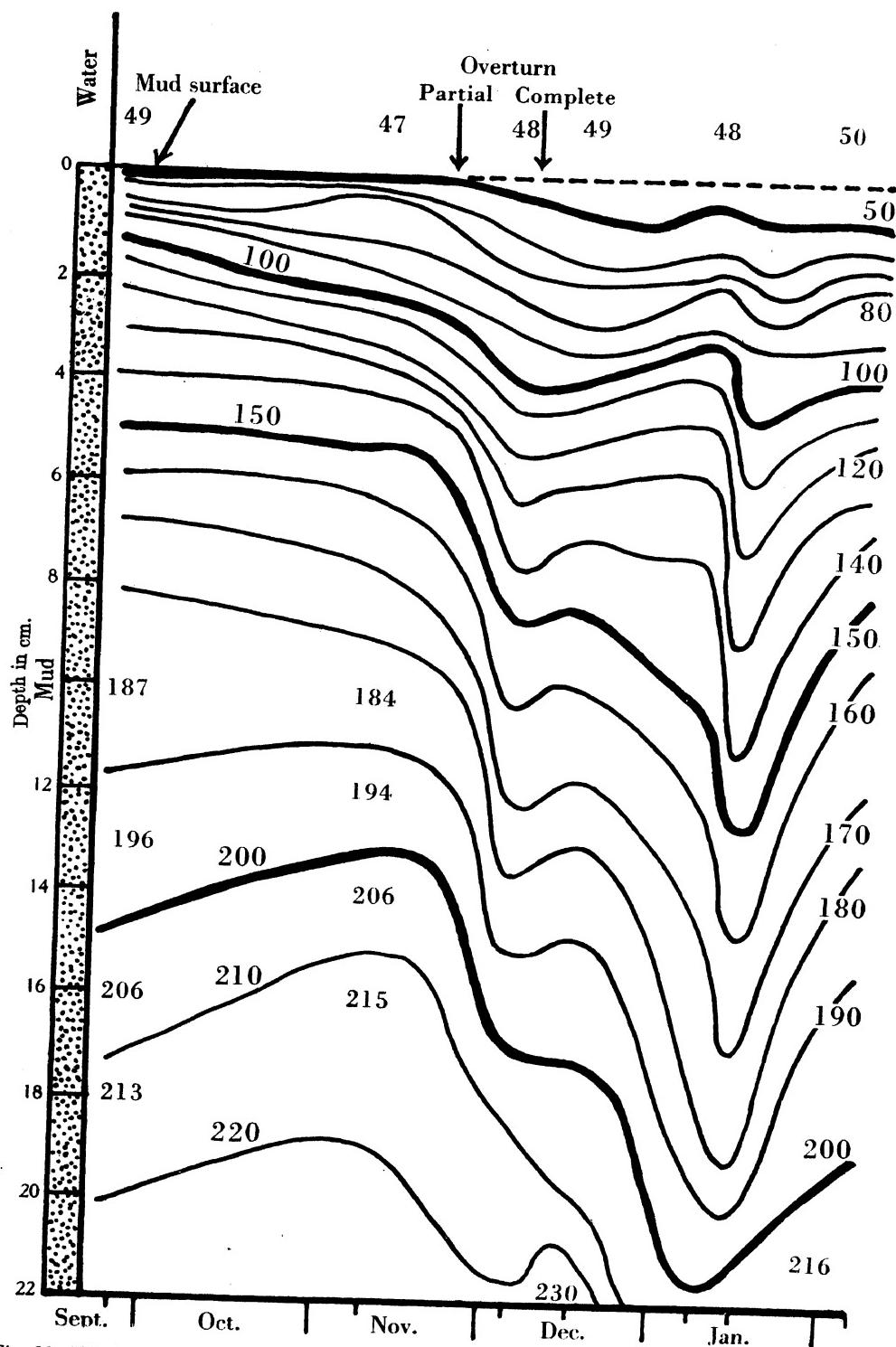


Fig. 33. Windermere, North Basin, 1940-1. Depth-time diagram of the distribution of electrical conductivity above and below the mud surface, 65 m. ( $K_{18^\circ} \times 10^{-6}$ ).

hand, the marked seasonal changes, found to be associated with de-oxygenation of the hypolimnion and reduction of the mud surface in Esthwaite Water, were also demonstrated by a detailed study of conditions in water and mud of Blelham Tarn and also by the examination of occasional samples from

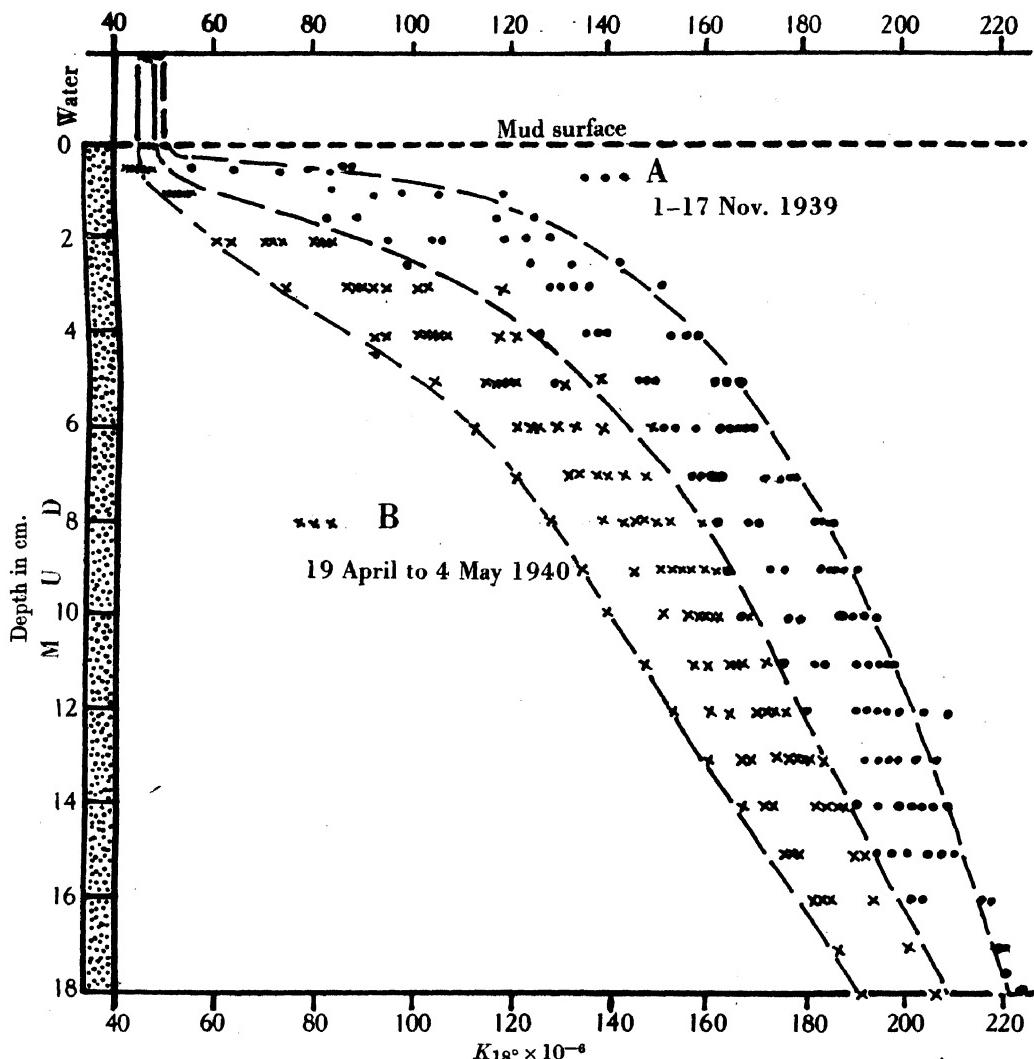


Fig. 34. Windermere, North Basin, 1939-40. Comparison of the distribution of electrical conductivity in surface mud cores, from depths greater than 50 m., (A) at the end of summer stagnation (autumn 1939, 8 cores), and (B) at the end of the circulation period (spring 1940, 9 cores). The overturn occurred about 20 November 1939.

other lakes in which de-oxygenation of the hypolimnion occurs (Rydal Water, Loweswater). This suggests that the conditions found in Windermere and Esthwaite Water may be considered as representative of two fundamentally

different lake types. The causes of these differences and their relation to organic production will be discussed in § IV.

*Discussion of the results from Esthwaite Water.* The considerable increase in the concentration of certain solutes in the water over the mud, which

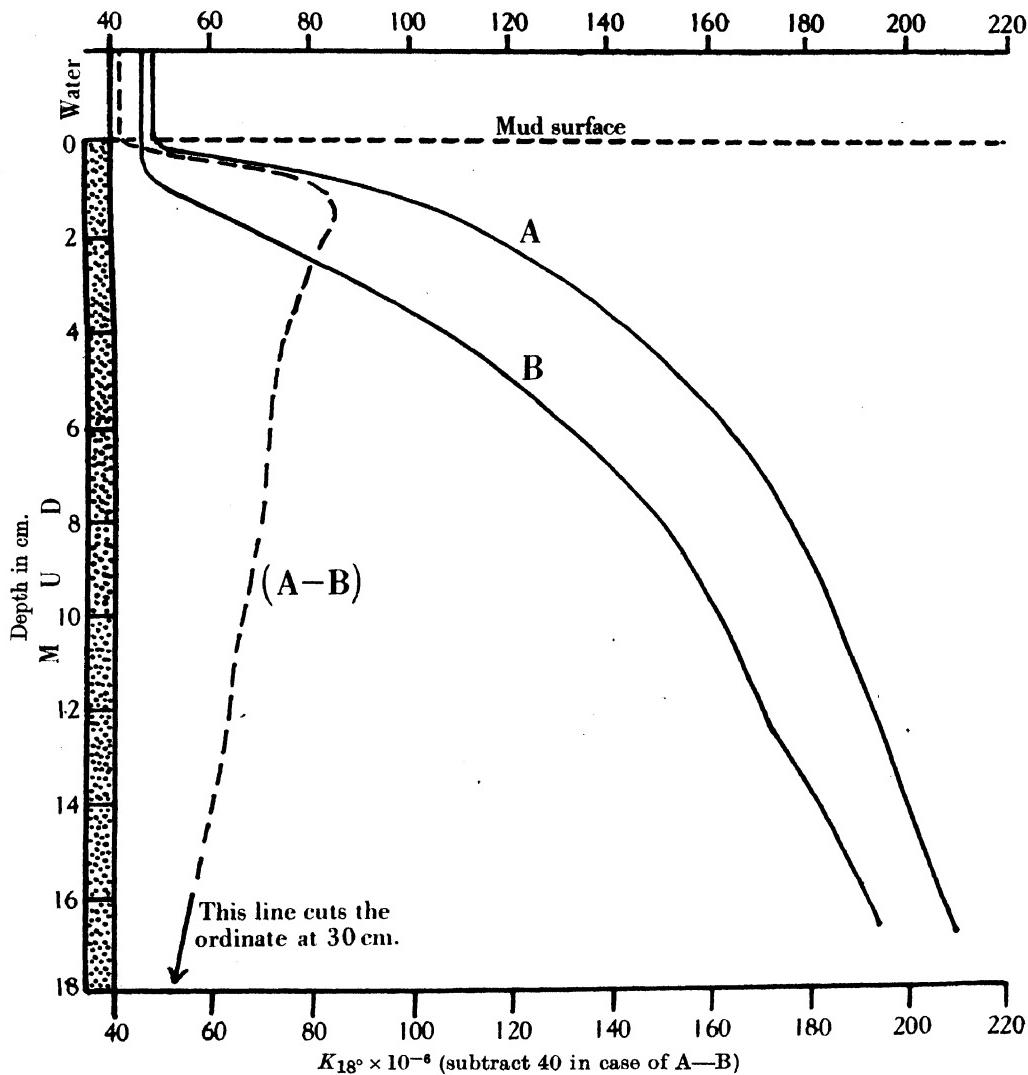


Fig. 35. Windermere, North Basin, 1939–40. Mean distribution of electrical conductivity—computed from Fig. 34—in surface mud cores, from depths greater than 50 m., (A) at the end of summer stagnation (autumn 1939) and (B) at the end of the circulation period (spring 1940).

occurred after the mud surface had become reduced—or, more precisely, after the isovolt  $E_7 = 0.20$  V. had risen to the mud surface—is in close agreement with the findings in the anaerobic tank experiment (§ II), and substantiates

the suggestion, made in § I, that similar increases observed in 1939 resulted from the reduction of adsorbing ferric complexes in the mud surface. In short, results from all three sections are consistent with the view that comparatively large amounts of material are liberated during the destruction of the oxidized surface mud layer. The rate of increase in concentration of many substances in the water during the later summer was usually much slower. This may be taken to represent the steady rate of supply from continuous processes in the mud, the products of which were free to diffuse into the water unhampered by the strongly adsorptive effect of the oxidized mud surface.

In contrast to this, conditions (*a*) in Esthwaite Water after the overturn when the surface oxidized layer had re-formed, and (*b*) in Windermere, where the oxidized layer was never completely destroyed throughout the year, were similar to those observed in the aerated tank (§ II). Although continuous production of ions must have been taking place, concentration in the water was little affected, as precipitation and adsorption in the oxidized mud surface had immobilized a large part of these products. This process, and its reversal after the onset of thermal stratification, also appears to have affected ionic concentration in the mud itself. Thus the general rise in conductivity of the mud in Esthwaite Water during May and June (Fig. 30) may be attributed to the decrease in thickness of the oxidized layer, resulting in the liberation of adsorbed ions and to a corresponding decrease in capacity of the surface layer to adsorb products of continuous mud processes. A converse explanation may apply to the general fall in conductivity after the overturn. It appears unlikely that these changes can be explained by changes in temperature at the mud surface, as this was fairly constant throughout spring and early summer, rising to a maximum at the overturn. This rise in temperature might be expected to increase ionic production in the mud; but in fact a decrease in conductivity occurs at this time. Similar seasonal changes in the conductivity of Windermere muds (Fig. 33), although not so marked as in Esthwaite, may be considered to be associated in a similar manner with changes in thickness, and therefore in total effectiveness as an adsorbent blanket, of the surface oxidized layer.

It will be observed that both in Esthwaite Water and Windermere (Figs. 30, 33, 34, 35) the greatest changes in the concentration (conductivity) gradient occurred at and near the mud surface, suggesting that the amplitude of seasonal fluctuations is greatest in this region. These fluctuations may be considered to result partly from the physical-chemical changes in the mud surface, described above, and partly from seasonal changes in the eddy diffusion coefficient in the water just above the mud. The *rate of removal* of ions from the mud depends on the product of this coefficient and the concentration gradient in the water in contact with the mud.

The reason for the rise to the high conductivity maximum observed at

the mud surface on 24 July (Fig. 30) is obscure. The oxidized layer was destroyed and the ions adsorbed in it presumably released a month earlier. These high values cannot be due to contamination, as they were found on two sampling occasions, and their effect on the mud surface is apparent for some time afterwards. It is possible that a large plankton crop produced during the long calm fine spell in the latter half of July may have settled and decomposed on the mud surface. Unfortunately, no data on the plankton population is available. The fall in conductivity after this period may have been the result of diffusion of the products of this decomposition into the water, in which a marked increase in conductivity was noted at this time, and also partly to the cause, to which a similar fall in conductivity in the anaerobic tank was attributed (§ II), namely, precipitation of ferrous sulphide. The fall is greatest in the top few centimetres of the mud, in which most precipitation might be expected to occur, and in which considerable accumulations of black ferrous sulphide were observed towards the end of the summer.

Fluctuations in conductivity throughout the whole mud core at the time of the overturn are difficult to explain. The partial overturn (23 September) was associated with a fall in conductivity, another rise occurring during the period before complete circulation of the bottom water had been established (cf. Figs. 27, 30). This was followed by a sharp fall, then a slight rise and a slow fall during the early winter. Without further study it cannot be said how far these variations may be attributed to local variations near the sampling point. Such variation is, however, relatively small in the deep region of Windermere (Fig. 34). If local variation is made responsible for the fluctuation observed during the month ending 21 October, it is difficult to explain why such fluctuations were not observed at other times of the year.

The explanation of the rise in conductivity which occurred in the mud during the period under ice is considered to be the same as that given for the similar rise which occurred during May and June. Partial reduction of the mud surface and decrease in eddy diffusion in the water over the mud were probably both contributory factors. If the results from one sample (15 February) are considered to be representative, the rise in mud conductivity under ice was greater than during a comparable period in the spring. This cannot be explained by a more rapid reduction of the mud surface under ice (cf. Figs. 28, 30), but must have been the result of the difference in eddy diffusion coefficient in the water just above the mud during the two periods. Under ice this coefficient was certainly considerably lower than during summer thermal stratification (cf. Tables 1 and 2, § I).

Other points of interest arising from changes in the distribution of redox potential and concentrations of dissolved substances are briefly dealt with below. The lag (Fig. 28) in the formation, after the overturn, of a surface-oxidized layer, comparable in thickness to that found at the end of the winter, may be considered to be the result of the slowness of diffusion in the mud

and of the slowness of oxidation of the accumulated products of summer reduction. Of these, ferrous sulphide probably forms an important part. Similarly, the lag in reduction processes during the initial stages of summer stagnation (Figs. 12, 28) may be largely due to the slowness of reduction of ferric hydroxide and other ferric complexes under natural conditions. A similar observation was made by Pearsall & Mortimer (1939, p. 493).

No explanation can be offered for the large fluctuations in concentration of some substances, notably phosphorus, iron and reducing substances ('oxygen demand') in the water above the mud during summer. Such large fluctuations were not observed during 1939. It is probable that, compared with 1939, conditions in the hypolimnion were unstable as a result of poorly developed stratification (cf. Figs. 3, 26). August was also exceptionally stormy. However, estimates of the eddy diffusion coefficient for that month at 13 m., obtained by methods described in § I, are not considerably greater than estimates for a similar period in 1939 (see Table 1, § I). The mean estimates of [A] for August 1940 and 1939 may be taken as  $4 \times 10^{-2}$  and  $3 \times 10^{-2}$  respectively.

A comparison of the graphs of  $O_2$  and  $CO_2$  concentrations (Fig. 29) suggests that little, if any, anaerobic  $CO_2$  production occurred.

In most natural waters manganese, like iron, is practically insoluble in trivalent (oxidized) form, but is soluble in manganous (reduced) form. The appearance of manganese in the water at an earlier date than ferrous iron, and its persistence for some time after ferrous iron had disappeared at the overturn, suggests that insoluble manganic compounds in the oxidized mud surface are reduced more readily, i.e. at a higher redox potential, than the ferric complexes. It is of interest to note that sulphate, although considerably depleted, was not completely reduced in the water above the mud during summer stagnation. It may also be noted that the redox potential in the water did not reach the potential,  $E_7 = 0.06$  V., at which sulphate completely disappeared in the anaerobic tank experiment (§ II), until just before the overturn.

Chloride showed little seasonal change in concentration (Fig. 29). This agrees with the findings of Ohle (1933-4). The chloride ion is apparently not concerned in seasonal redox and associated changes.

The results obtained on Esthwaite Water 1940 have confirmed the description of events in the hypolimnion, suggested by the study of the distribution of redox potential and dissolved substances in the water during 1939 (§ I). Seasonal changes in the mud are correlated with and largely control seasonal changes in the water. In particular, variations in concentrations of solutes in the hypolimnion, detected during 1939 and confirmed during 1940, were found to be dependent on redox conditions at the mud surface. Almost all the phenomena in mud and water, described during the development of anaerobic conditions in an artificial mud-water system (§ II), were found to

be repeated in the same order in Esthwaite Water during the development of de-oxygenation in the hypolimnion. One exception was that the complete reduction of sulphate with precipitation of ferrous sulphide in the water, observed in the experimental tank, did not occur in Esthwaite Water during 1940, although there is some evidence that it occurred during September 1939. This may be explained by the higher mean potential in the lower hypolimnion during September 1940. The mean potential at 13 m. during the month preceding the overturn in 1940 and 1939 was approximately  $E_7=0.17$  and 0.09 V. respectively. The latter potential is not far removed from that ( $E_7=0.06$  V.) at which sulphate disappeared from the water of the experimental tank. The reason for this difference in behaviour between successive years may have been the conditions under which thermal stratification was set up in the spring. From the outset the hypolimnion was thermally stratified to a far higher degree during 1939 than during 1940 (cf. Figs. 3, 26).

*Discussion of results on Windermere.* If the explanation of events in Esthwaite Water is a true one, then the fact that the surface oxidized layer of the mud was not reduced in Windermere explains the absence of large seasonal variations in concentrations of dissolved substances in the water. The relatively high concentration of dissolved oxygen, which was maintained at the mud surface during the period of thermal stratification, was responsible for the failure of the lower mud—the reducing intensity of which, as will be shown later, is not far below that of Esthwaite Water—to reduce the ferric complexes in the mud surface. When, under suitable conditions (anaerobic tank experiment), reduction of Windermere surface mud did take place, marked changes occurred in the mud-water system similar to those already described for Esthwaite Water. The small seasonal variations which were found to occur under natural conditions in Windermere are probably largely the result of seasonal changes in degree of eddy diffusion and in oxygen concentration gradient at the mud surface.

The thickness of the surface-oxidized mud layer may be taken to represent a balance between (a) the rate of diffusion of oxygen into the mud, which is a function of the concentration gradient at the mud surface, and (b) the reducing power of the mud. Seasonal variation of (b) is not known, but probably not large. When the rate of supply of oxygen to the mud surface by eddy diffusion from above is decreased during thermal stratification, the concentration gradient at the mud surface decreases to an extent determined by the degree of eddy diffusion in the water and the rate of oxygen absorption by the mud. The thickness of the surface-oxidized layer then decreases, adjusting itself to the new balance between oxygen supply and consumption. It is possible that the slowness with which insoluble ferric compounds are reduced imposes a lag on this adjustment. The decrease in thickness, of course, takes place from below, and may be expected to result in some liberation of soluble ions previously adsorbed or precipitated (Fe, Mn,  $\text{PO}_4$  and bases), and also in

some depletion of the total capacity of the oxidized layer to bind the products of continuous processes in the lower mud. One demonstrable result of this is a rise in ionic concentration (conductivity) in the mud and a slight increase in concentrations of certain substances (cf. alkalinity, conductivity,  $\text{CO}_2$ ) in the water. The bulk of the material liberated in this way, however, is re-absorbed by the surface oxidized layer that remains. The main difference between lakes of the two types, exemplified by Esthwaite Water and Windermere, is that in the former the supply of dissolved oxygen to the mud surface is more limited and the oxygen concentration gradient falls sufficiently low for the whole of the surface oxidized layer to become reduced, initiating the marked changes in ionic exchange between mud and water, already described.

At the overturn both lake types exhibit a reversal of the changes which took place in mud and water during thermal stratification. The reversal in the mud appeared to be more rapid in Windermere than in Esthwaite (cf. Figs. 28, 32). This may be because no considerable sulphate reduction and accumulation of insoluble ferrous sulphide in the mud surface occurred in Windermere.

#### IV. GENERAL DISCUSSION

Facts and correlations disclosed by the findings in preceding sections, and further data obtained from other lakes in the English Lake District, linked together by hypothesis, help to provide a description in outline and in physico-chemical terms of one aspect of the cycle of organic production in lakes. Roughly speaking this description applies to a reversible system, the chemical cycle in the lake basin, which is inserted into and maintained by a larger relatively irreversible geochemical process, enacted in the whole drainage basin. As a hydro-electric plant transforms and accumulates a portion of potential energy, which would otherwise be (relatively) irreversibly wasted, so a lake traps for organic production a part of the available 'chemical potential' of a drainage system, which would otherwise be more rapidly lost to the sea. Various factors, including the peculiar properties and stability of humus, normally lead to the accumulation of organic material in lake deposits, which function as accumulators, defraying a portion of the 'chemical potential' for organic production in the water, and themselves being continually replenished by deposition of organic matter and silt from above. Thus anabolic processes in the water and katabolic processes in the mud constitute a reversible lake system, the importance of which, relative to irreversible maintenance processes in the drainage area, may be expected to vary with the age of the lake and the ratio of its water volume to inflow. The constitution of the mud-water-atmosphere system, and the fact that katabolic processes involve reduction, explains why redox reactions are so intimately linked with the lake cycle. The impact of climate on the system exercises a profound influence through control of the seasonal distribution of redox conditions.

One general result of this investigation has been to direct attention to the importance of (a) processes in the mud, especially at the mud surface, and (b) water movements, for the 'metabolism' of the lake as a whole. Both these aspects of the lake cycle have received some special discussion in previous sections. In particular, the importance of the presence or absence of reduction at the mud surface, discussed in terms of colloid chemistry, was emphasized especially in §§ I and II, while the controlling influence of turbulence, associated with water movements, on the transport of dissolved substances within the lake system was demonstrated in § I. Apart from some further discussion of water movements, this section therefore will be confined to a consideration of some general implications of the previous findings.

*Biotic influences.* It will be noted that the interpretation of the changes observed in both natural and artificial mud-water systems in previous sections has been almost exclusively physico-chemical. Biotic influences must not be ignored, although the closeness with which a relatively simple physico-chemical interpretation fits the facts suggests that these influences express themselves mainly along physico-chemical lines. Among such influences may be included the relation of bacterial population and its activities to redox conditions (see Hewitt 1931 for a review of this subject) and the effect of plankton production on the rate of addition of organic matter to the hypolimnion and mud. The effect of changes in the distribution of physico-chemical variables on organic reactions should also be considered. A beginning has been made by Kusnetzow & Kusnetzowa (1935), who found that the bacterial reduction of formic acid to methane took place most actively in muds at a redox potential of  $E_7 - 0.12$  V., and that the upper potential limit was between  $E_7 0$  and  $+0.15$  V. Active methane production, however, was not found in all muds below these potential limits. They suggested that C and N supply is the controlling factor.

*The relation of seasonal variations in redox conditions at the mud surface to the ecology of the profundal bottom fauna.* It appears highly probable, but still remains to be demonstrated, that a close relationship of this kind exists. Since the classical work of Thienemann and collaborators, a relation between the profundal bottom fauna, especially Chironomidae, and degree of productivity (trophic condition) in lakes has been established. Hutchinson *et al.* (1939) discuss certain inconsistencies that have been found, suggest that redox potential is an important determining factor, and demonstrate a relation between the Chironomid population in a series of lakes and the redox potential of the bottom water during thermal stratification. In the absence of potential measurements in the muds, they consider the reducing power of the mud only as it affects the open water. It should be noted that the potentials recorded in the presence of ferrous iron (detected by  $\alpha$ - $\alpha'$ -dipyridyl) are considerably ( $0.1$ - $0.2$  V.) higher than those found in the presence of similar  $\text{Fe}^{++}$  concentrations in Lake District lakes and artificial mud-water systems (cf.

previous sections and also the discussion of the determination of  $\text{Fe}^{++}$  by this method, Hutchinson 1941). As a result of a quantitative study of the ecology of the profundal bottom fauna in lakes, Eggleton (1931) concludes: 'Emergence and egg laying of insects, variations in sexual activity of other benthic types, and the rate and time of hatching of eggs on the lake floor are all influenced by the physical-chemical seasonal cycle and, in turn, greatly affect the qualitative-quantitative variations of the profundal benthic population.'

#### *Water movements*

Before proceeding to a discussion of the factors which determine whether or not reduction of the mud surface and associated physico-chemical changes take place, present knowledge of water movements in the hypolimnion must be considered. The position is unsatisfactory in so far as all evidence of the nature of these movements is *indirect*. Technical difficulties have so far prevented actual measurement of their velocity and direction. Although all such indirect evidence from the rate of change of distribution of dissolved substances and temperature agrees in demonstrating that the hypolimnion is not stagnant, the views so far expressed on the cause and nature of the water movements show disagreement.

The predominant effect of wind in distributing heat in regions of lakes removed from the effect of radiation was originally recognized by Murray (1888, refs. in Murray & Pullar, 1910). This theory of wind-distributed heat was amplified by Birge (1916), who, in common with Schmidt (1925, 1928), regarded turbulence associated with wind-generated currents as the main agent in transporting heat and dissolved substances throughout lakes, including the hypolimnion. McEwen (1929) has attempted to establish a practically complete and therefore complex mathematical theory of the distribution of temperature and dissolved substances in natural waters, taking radiation, conduction, evaporation, convection and wind-generated turbulence into consideration. A general result emerging from the application of this theory to the distribution of temperature in Lake Mendota was that the effect of all factors except the last was found to be practically confined to the epilimnion and the thermocline region. This theory is discussed in detail by Hutchinson (1941).

The above authors have little to say on the generating mechanism and magnitude of the water movements producing turbulence in the hypolimnion. One over-simplified view often expressed (cf. Wedderburn, article in Murray & Pullar, 1910; also Whipple, 1927, ref. in Welch, 1935), is that wind produces a surface drift compensated by a return current in the lower part of the epilimnion, which in turn induces a slower circulation in the hypolimnion. Whipple actually demonstrated that a return current may also occur in part below the thermocline. But the marked chemical stratification encountered in the hypolimnion of many lakes (cf. results for Esthwaite Water) is not concordant with the view that this secondary circulation below the thermo-

cline involves a *complete rotational motion* (overturn) of the hypolimnion water mass of the type figured by Wedderburn (Murray & Pullar, 1910). This has been emphasized by Alsterberg (1927, 1930), who considers that the primary circulation in the epilimnion induces a secondary circulation in the upper hypolimnion, which in turn induces a tertiary one at a lower level, and so on. He envisages a large number of such circulations moving in thin *horizontal laminae*, the resultant motion having a negligible vertical component. Although this hypothesis explains the preservation of chemical stratification, it is difficult to see how such a complex system of horizontal streaming, the direction of which is reversed at short depth intervals, could be set up and what source of energy is available to maintain it.

A discussion of Hutchinson's (1938b) evidence in favour of Alsterberg's views is relevant here, as he suggests that these views are contradictory to those which lay emphasis on turbulence. In the opinion of the present writer this disagreement is not a real one. First considering Hutchinson's evidence, this is based on a mathematical analysis of the vertical distribution of alkalinity in Linsley Pond (max. depth 14.8 m., area 0.094 km.<sup>2</sup>), a small eutrophic lake in which the rise in alkalinity in the hypolimnion is mainly due to the supply of ammonia and ferrous iron from the mud. As pointed out by Alsterberg himself, one of the deductions from his hypothesis is that a relationship should exist between the chemical characters of each horizontal layer of water and the area of mud surface to which it is exposed at the edges. This implies the unimportance of vertical turbulent transport relative to horizontal streaming, i.e. change in concentration at any one point in the hypolimnion water-column results, not from transport from above or below, but from the side. Throughout the whole of the summer Hutchinson found that the vertical concentration gradient of alkalinity was considerably less at two levels, usually approximately at 8 and 11 m., than at levels just above and below these. In other words, the concentration increased with depth, not in a smooth curve of the type to be expected if uniformly distributed eddy diffusion was responsible for the vertical transport of alkalinity, but in a series of steps. An apparent correlation existed between the form of this latter curve and a curve which represented the depth distribution of the relative areas of mud to which each horizontal layer of water was exposed at its edges. In Hutchinson's view this correlation supported Alsterberg's hypothesis and excluded the possibility of vertical turbulent transport.

This conclusion is open to question on the following general grounds. In order to produce the observed rate of increase in concentration at the (central?) sampling station, horizontal streaming, to be effective in transport over the distance from the side (area of lake is equivalent to a circle of radius 173 m.), would almost certainly have been sufficiently rapid to involve turbulence. This argument would apply more forcibly to a larger lake. It is also shown later in actual examples (Figs. 37, 38, 39 and 41) that isotherms and isopleths

may be forced out of their normal horizontal position. Such displacement would disturb purely horizontal laminar flow. Hydrodynamical theory (Schmidt, 1925; Defant, 1929) postulates that water movements under open unstratified conditions are associated with turbulence even at extremely slow velocities. Pure laminar flow may be expected hardly ever to occur. This being so, the apparent disagreement between Alsterberg's hypothesis and the 'turbulence hypothesis' disappears. Both views stress different aspects of the same phenomenon. It is clear that, as Alsterberg and Hutchinson emphasize, movements of water masses in the hypolimnion must be mainly horizontal; nevertheless the turbulence necessarily associated with these movements would be sufficient to account for the vertical transport of solutes (which Alsterberg has demonstrated is more rapid than would be the case if molecular diffusion alone were operative), and also for the maintenance of chemical stratification, as long as the dimensions of the turbulent eddies are small in comparison with the hypolimnion.

Discussing hypolimnion water movements in more detail, Hutchinson (1941) modifies his former extreme view (1938b), admits the presence of turbulent mixing, but considers it inadequate in accounting for the observed distribution of temperature and alkalinity in the lower hypolimnion of Linsley Pond, Lake Quassapaug and Lake Mendota. Data for Lake Mendota (area 39 km.<sup>2</sup>, max. depth 23.5 m.) was obtained from Birge's computed mean weekly temperature distribution for 1895–1915, as used by McEwen (1929). Much of Hutchinson's subject-matter, especially that describing the phosphorus cycle and development of chemical stratification in Linsley Pond, has considerable bearing on matters discussed here. A more detailed consideration, however, must be deferred, apart from an outline of the argument with regard to water movements, which follows.

If it be assumed that (i) the distribution of heat in the water column during spring and summer is effected wholly by turbulent transport from above, and that (ii) a constant eddy diffusion coefficient ( $A$ ) is maintained throughout the column, then the rate of change of temperature ( $d\theta/dt$ ) in the column falls exponentially with increasing depth ( $z$ ). In the above lakes such a region of exponential fall of  $d\theta/dt$  is confined to the upper part of the hypolimnion, termed *clinolimnion*, which may include part of the thermocline. Departure from the exponential fall in the epilimnion forms the basis of McEwen's (1929) theory of convectional cooling, and cannot be discussed here. Departure in the lower hypolimnion—or *bathylimnion*, in which  $d\theta/dt$  tends to become constant at all depths—is the subject of present discussion. This departure implies that, in part of the bathylimnion at least, either (a) the eddy diffusion coefficient increases with depth, or (b) some other non-turbulent heating mechanism is operative. Hutchinson accepts the latter alternative on the following grounds.

Mathematical analysis of temperature distribution by McEwen's (1929)

method (i.e. fitting the observed vertical temperature gradient,  $d\theta/dz$ , to an arbitrary function which can be simply differentiated) yields mean estimates of  $A$  for different levels. These estimates vary little in the clinolimnion (4–9 m. in Linsley Pond, 9–16 m. in Mendota) with either depth or 'stability' (i.e.  $d\sigma/dz$ , where  $\sigma$  = density). From this, Hutchinson infers that 'the generalization that the coefficient of turbulence is minimal in the more stable layers is clearly erroneous as far as the clinolimnion... is concerned. Moreover, if as seems probable, the coefficient is essentially constant throughout the whole hypolimnion, the generalization is essentially false for all depths below the thermocline.' In other words, he does not expect turbulence to increase in the lower hypolimnion as a result of the decreased stability there. However, assuming alternative (a) and the exclusion of (b), and using methods similar to those used to obtain estimates of  $A$  in § I, Hutchinson does in fact arrive at values which, in the case of Lake Mendota, increase from  $3 \times 10^{-2}$  c.g.s. units in the clinolimnion to double this value at 20 m. depth. Nevertheless, he concludes: 'Since, at least in [his] Figure 4, the criterion of validity [applied by McEwen 1929, demonstrating constant  $A$  in the clinolimnion] is so clearly satisfied, it is certain that these increasing values are erroneous.' (Brackets and italics inserted in above quotations by present writer.)

Clarification of this point is important, for, if Hutchinson's view is correct and of general application, the estimates presented in Tables 1 and 2, § I, may not represent true coefficients of eddy diffusion. The following considerations, however, prevent the ready acceptance of Hutchinson's views and their general application without further evidence. The 'criterion of validity' in the figure referred to above only applies to a depth of about 15 m., i.e. to the clinolimnion. There is not sufficient evidence for the assumption that, because  $A$  varies little with stability or depth in the clinolimnion, there is no variation in the bathylimnion and no correlation with stability. Hutchinson did in fact observe a marked decrease in  $A$  with increasing stability as the season advanced. It appears to the present writer that, pending further evidence, the decision between alternatives (a) and (b) is still open, and that, in view of the difficulties in the way of (b), discussed below, (a) is the more probable.

As a non-turbulent heating mechanism in the bathylimnion, Hutchinson suggests 'profile-bound chemical density currents', combined with horizontal streaming, presumably of the type postulated previously (1938b). He supposes that water in contact with the mud, as a result of its increased dissolved content (1 mg./l.  $'\text{HCO}_3'$  was equivalent to a density increase of  $1.8 \times 10^{-6}$  in Linsley Pond), flows down the mud slope to its new density level, carrying heat with it. This mechanism has been suggested (Birge *et al.* 1928) to explain the warming of the bottom water of lakes under ice to temperatures above  $4^\circ \text{C}$ . In discussing the possible effectiveness of such a mechanism it should be remembered that in most lakes the mud slope in the deep regions is very slight. It is therefore open to question whether the small density increase

produced in the water in contact with the mud is sufficient to overcome the friction offered by the mud surface. Hutchinson does not discuss the location of the compensation flow necessarily resulting from such 'chemical density currents', but, as horizontal streaming is held responsible for transport from the mud slope to the lake centre, it is possible that he envisages a central upward compensation flow of the type suggested by Alsterberg. Difficulties in the way of conception of a purely horizontal laminar flow were discussed earlier.

In § I a method of computing exchange coefficients at certain levels in the hypolimnion water column, from the transport of heat downward and of solutes upward through these levels, was applied. Examination of this method and its preliminary assumptions shows that the estimates obtained were of 'virtual' exchange coefficients and yielded no information on the exchange mechanism. Now if this mechanism is mainly turbulence, estimates obtained from the transport of *any* conservative property through the level, i.e. transport of heat downwards and of various solutes upwards, should be identical. On the other hand, one result of Hutchinson's non-turbulent exchange mechanism, whether operative alone or superimposed on turbulence, is a flow of heat and solutes down the mud slope and from there, by horizontal streaming, to corresponding levels of the central water column. It follows that the 'virtual' exchange coefficient at any level in this column, computed, as in § I, from the *downward* transport of heat, will be greater than those estimates computed from the *upward* transport of solutes. In Esthwaite Water and Schleinsee (Table 1) the reverse was found to be the case, although the estimates can only be regarded as first approximations using inadequate data. Agreement between estimates from upward transport of various solutes was satisfactory; lower values computed from the downward transport of heat may possibly be explained by failure to account for flow of heat into the mud. This discrepancy disappeared when the *upward* transport of heat and solutes in lakes under ice cover was considered (Esthwaite Water, Blelham Tarn, Table 2).

If, in view of these results, and in the absence of more detailed evidence, alternative ( $\alpha$ ), i.e. vertical variation in the eddy diffusion coefficient, is accepted as an explanation of the distribution of heat and solutes in the hypolimnion, then the 'stepwise' increase in alkalinity with depth in Linsley Pond (Hutchinson, 1938b; cf. also Esthwaite Water, Figs. 7, 11) is primarily determined, not by any apparent correlation with the depth distribution of mud area, but by depth variation of  $A$ . Another factor which influences the depth distribution of alkalinity, and also limits its application as a 'conservative' property in turbulence computations, is the oxidation of ferrous iron at the top of the hypolimnion, the re-solution of the precipitated ferric hydroxide at lower levels, and adsorption phenomena associated with this. It is of interest that Hutchinson *et al.* (1939) found the thermocline in Linsley Pond at 7 m.

depth on 16 September 1938, i.e. 1 m. above the upper 'step' in the alkalinity depth distribution curve (Hutchinson, 1938b).

To summarize this discussion: results to date demonstrate that water flow in the hypolimnion is largely horizontal, permit the expectation that turbulence associated with this flow is the main mechanism of heat and chemical exchange in larger lakes, and suggest that non-turbulent exchange mechanisms may become increasingly significant in smaller bodies of water. A probable cause of the horizontal flow is described below.

*Suggested mechanism of induction of horizontal water movements in the hypolimnion.* Murray (1888, refs. in Murray & Pullar, 1910) was the first to demonstrate, from the study of vertical distribution of temperature at various points along an axis of a lake, that a wind blowing in one direction for some time across a thermally stratified lake may transport warm surface water to the lee side, resulting in a deepening of the epilimnion on that side and a corresponding tilt of the isotherms in the thermocline region. When the wind drops, this tilt is clearly unstable. The isotherms swing back to horizontal. They may swing past the horizontal level of equilibrium and set up a series of oscillations or 'temperature seiches'. Wedderburn (1911) has shown that the theoretical frequency of such oscillations may be estimated from a consideration of ideal lake systems in which the discontinuity layer between two fluids of different density oscillates in a similar manner. The theory has also been applied to a stratified liquid of varying density in basins of different shapes. Close agreement was obtained between the frequency computed from theory and that observed in Loch Earn and in experimental tanks (Wedderburn, 1912). The appearance of temperature seiches in Loch Earn and in other lakes was found to be related to wind and other meteorological conditions. Correlation between wind and temperature oscillations was close in most cases, but not so complete in others. 'Examples of the effects of winds, both in starting and in damping oscillations already in progress, have been given, with the indication that even a wind of *very moderate strength* will start oscillations, and examples of oscillations forced by wind have also been obtained' (my italics).

It is clear from the observations of Wedderburn and others that a tilt of the thermocline, i.e. displacement of the 'isosteres' (surfaces of equal density) from the position of horizontal equilibrium, is a common occurrence which must result in some displacement of the hypolimnion water mass. The extent and path of the resultant motion is at present largely unknown, but it may be suggested from theory (Defant, 1925, pp. 24-5, Figs. 4, 5) and from tank experiments (Wedderburn, 1911, Pt. I; Wedderburn & Williams, 1911; Hutchinson, 1938b) that an *oscillatory* motion is induced in phase with changes in declination of the isosteres, and that in the central region of the lake basin this motion is mainly horizontal or parallel to the contours of the bottom. In direct attempts to measure flow in the hypolimnion of Loch Earn it was

found that the currents were too slow to be detected with an Ekman current meter, i.e. they were less than 1 cm. per sec., below 20 m.

If, as seems probable, the flow induced in the hypolimnion by wind-generated displacements of isosteres has the character of discontinuous, damped, horizontal oscillations, and is not a unidirectional laminar streaming of the Alsterberg type, then this is an additional reason for the expectation that distribution of properties in a central hypolimnion water column is controlled mainly by vertical transport due to turbulence resulting from these oscillations, and not by lateral transport from the mud slope to which, if projected horizontally, each slice of the water column is exposed at its edges (cf. Hutchinson, 1938b). Further, there is nothing inherent in the mechanics of isostere displacement to suggest that the coefficient of turbulence is constant at all depths, in fact the contrary may be expected.

Evidence of the effect of wind in tilting isotherms and isopleths is presented in Figs. 37, 38, 39 and 41, but the direct demonstration of horizontal oscillatory flow in the hypolimnion and of turbulence associated with it has still to be achieved. As the movements are wind-generated, the rate of spread of properties in the water column may be expected to depend on the work done by the wind, i.e. on such factors as wind velocity, length of 'fetch' and degree of exposure of the lake. Murray (cf. Wedderburn's article in Murray & Pullar, 1910) noted that the temperature in the abyssal regions of deep lakes increased during the summer in 'fits and starts', depending on the occurrence of windy spells.

It can be shown that a relation exists between (a) the dimensions of the lake basin, and its exposure to wind, and (b) the mean eddy diffusion coefficient in the hypolimnion. A wind can exert a greater total force on a larger area, and the damping effect of friction with sides and bottom is less in a deeper lake. Rough estimates of a mean value of  $A$ , for periods of summer thermal stratification at certain levels in the hypolimnion, have been made for a variety of lakes, from temperature data by the method outlined in § I. These are presented, with morphometric constants for the lakes, in Table 4. The flow of heat into the deposits has been neglected. This involves an error which will be greatest for shallow lakes. Estimates of mean  $A$  for Esthwaite Water, obtained from other data (cf. Table 1), have been included for comparison. It may be concluded (Fig. 36) that the mean value of  $A$  in the hypolimnion during summer thermal stratification is roughly proportional to the magnitude of the lake. It cannot be stated whether either area, depth, or volume, is the controlling factor. However, correlation of  $A$  is closest with 'depth at the measuring station' (Fig. 36 B). Degree of exposure to wind is also clearly of primary importance. The low value in Lunzer Untersee in spite of its depth, for instance, may be a result of shelter in a steep-sided valley.

*Chemical evidence of water movements associated with wind-induced isostere oscillations.* In the few studies that have been made of the horizontal

Table 4. Comparison of (i) rough estimates of the mean value of the eddy diffusion coefficient ( $A$ ) in the hypolimnion of various lakes during periods of summer thermal stratification with (ii) the dimensions of those lakes

Lake	Key letter Fig. 36	Area km. <sup>2</sup>	Max. depth m.	Mean depth m.	Depth at measuring station m.	Rough estimate of			Sources of data
						$A \times 100$	For period	At depth m.	
Holsfjord	H	121	295	114	295	310	26. vi.-26. ix. 1930	100	Strøm, 1932
Geneva (large basin)	G	503	303	152	285	190	21. vi.-23. x. 1879	100	Forel, 1880, 1892
Lomond (Inversnaid)	L	71	195	37	185	53	22. ix.-14. xi. 1885	56	Buchanan, 1886; Murray & Pullar, 1910
Windermere, North Basin	N	8.2	67	26	55	39	14. vi.-13. ix. 1939	30	Taylor, 1940
Windermere, South Basin	S	6.7	44	18	30	9	6. vi.-20. ix. 1939	15	Mortimer (in prep. VI)
Mendota	M	39	25.6	12.1	23.5	7	15. vi.-15. viii. mean 1900-16	12	Birge <i>et al.</i> , 1928; Juday, 1914
Maxinkuckee	Ma	7.5	27	—	26	7	17. vii.-28. ix. 1900	18.5	Evermann & Clark, 1920
Kizakiko	K	1.4	29	—	25	5	June-Aug. 1926-9*	15	Yoshimura, 1936
Lunz; Untersee	Lu	0.68	34	20	32	5	29. iv.-29. vi.	20	Müller, 1938; Götzinger, 1912
Esthwaite Water	E	1.0	16	ca. 5	14	3	Cf. Table 1	12	This paper, also Mortimer (in prep. VI)
Schleinsee	Sc	0.15	11.6	6.4	11.6	2	Cf. Table 1	11	Einsele & Vetter, 1938

\* By inspection of isotherms in Fig. 6.

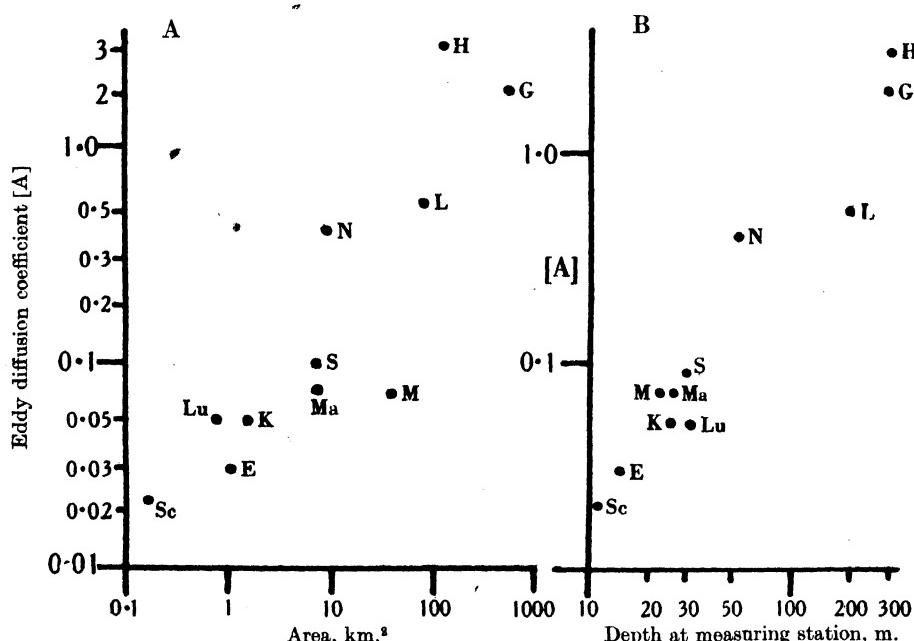


Fig. 36. A comparison of (i) the estimated mean values of the eddy diffusion coefficient  $A$  in the hypolimnia of various lakes with (ii) the dimensions of those lakes.

distribution of chemical variables in thermally and chemically stratified lakes (e.g. Rossolimo, 1931), a displacement of the isopleths from the horizontal, at the same time as a similar displacement of the isotherms due to wind action, has been frequently noted. Some observations in the Lake District have shown that this phenomenon may be produced by quite moderate winds. This is illustrated for a longitudinal section on Esthwaite Water in Figs. 37-39. Results for cross-sections on this lake were similar. It will be noted that the isopleths and isotherms exhibit a definite tilt as a result of a moderate wind blowing at the time. In addition, the oxygen isopleths in the hypolimnion were found to be depressed at the edges. This may have been the result of more intense mixing (due to friction with the bottom) on these slopes than at the same levels in open water, caused by the see-saw motion of the isopleths with changes in wind force and direction. The reducing power of the mud on the slopes may also be less than in the centre of the lake, as the adsorbent oxidized surface layer would be given a chance to form again if the surface was exposed to oxygenated water by a more pronounced or prolonged isopleth tilt than usual.

An example of such a tilt, and its readjustment to horizontal equilibrium after the wind has dropped, is illustrated by changes observed at two stations on Blelham Tarn (Figs. 40, 41), and was confirmed by observations at intermediate stations. After temperature measurements with a reversing thermometer, samples were taken at 0·1 m. intervals in the thermocline region by the following method. The surface mud sampler, described in § III, was lowered carefully to a selected depth in the thermocline region and closed. After raising, the top lid was removed and some liquid paraffin poured on to the water surface. By means of a special device samples were then siphoned simultaneously from each 10 cm. depth in the tube (discarding the top 10 cm.) into 50 c.c. bottles containing liquid paraffin to prevent the sample from coming into contact with air. Repetition of this technique at various levels, after moving the boat a small distance away from the disturbance caused by previous sampling, enabled the oscillation of the large concentration gradient to be demonstrated (Fig. 41). The final level of the thermocline (Fig. 41 B) was a little lower than the mean level during the rough spell. This represents work done by the wind, appearing as turbulence induced by the shearing of the epilimnion water mass over the hypolimnion, which must have occurred during the formation and subsequent decay of the tilt.

*The oxidized surface mud layer. Factors which control its thickness. Its relation to organic production, classification of lakes and lake evolution*

In a book, too comprehensive in scope for detailed consideration here, Grote (1934) raised many points of interest bearing on the work described in this paper. He deduces from theoretical considerations that, if the coefficient of diffusion of dissolved oxygen in the mud is assumed to be a constant, then the oxygen

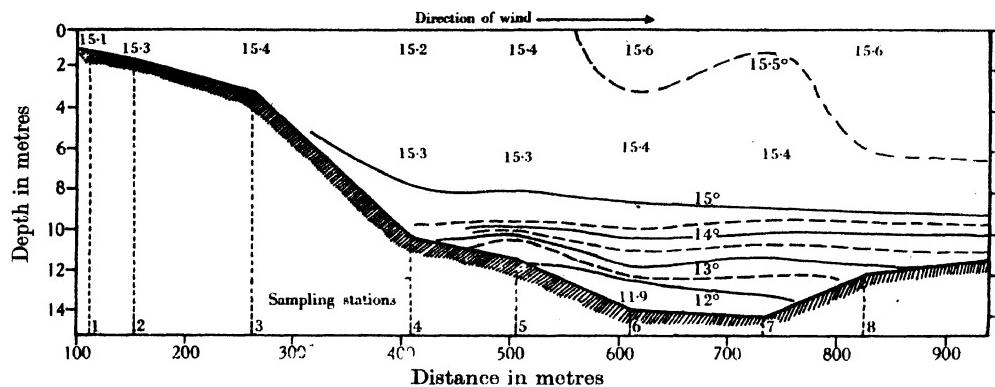


Fig. 37. Esthwaite Water. Distribution of temperature ( $^{\circ}$  C.) on a longitudinal section, 19 September 1939. Sampling stations on this section are shown on the map, Fig. 1, § I.

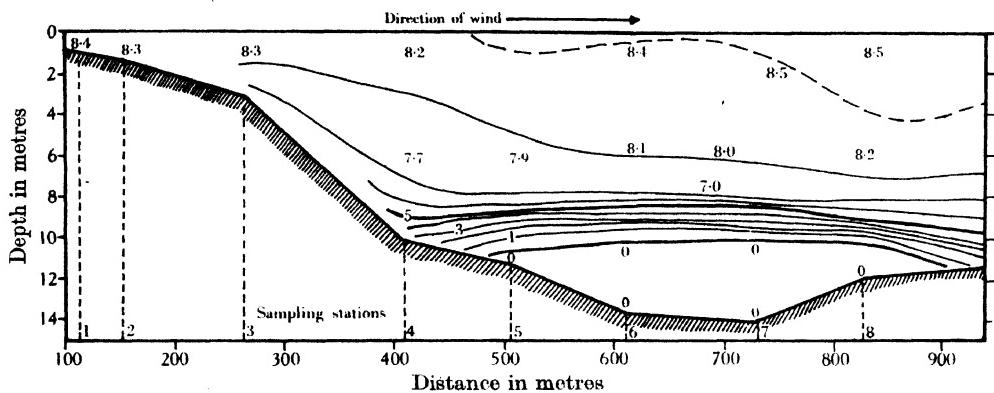


Fig. 38. Esthwaite Water. Distribution of dissolved oxygen (mg./l., unmodified Winkler method) on a longitudinal section, 19 September 1939.

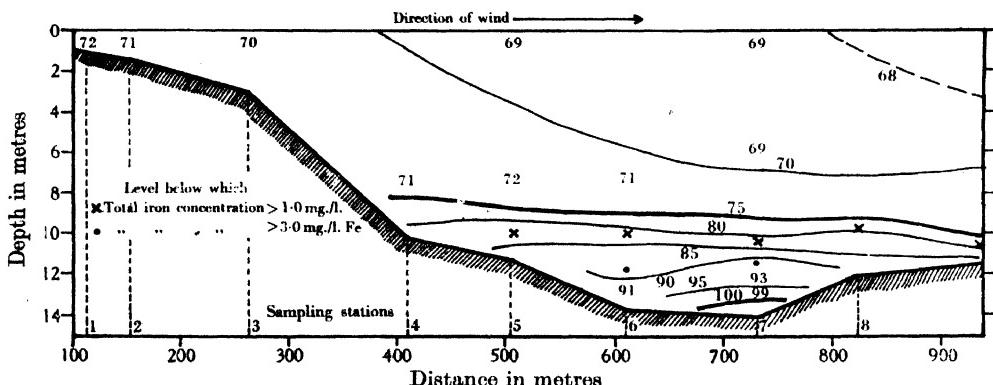


Fig. 39. Esthwaite Water. Distribution of electrical conductivity ( $K_{18^{\circ}} \times 10^{-6}$ ) on a longitudinal section, 19 September 1939. Also some data for iron.

concentration at the mud surface, divided by the thickness of the oxidized layer, roughly represents the mean oxygen concentration gradient maintained in the mud surface, and this must be proportional to the rate at which the mud absorbs oxygen. The thickness of the oxidized layer thus represents a balance between (a) the oxygen-absorbing power of the mud, and (b) the oxygen concentration at the mud surface. If (a), in comparison with (b), exhibits only small seasonal variation, the thickness of the oxidized layer, and whether or not it disappears, depends only on (b), i.e. the concentration of oxygen maintained at the mud surface. This will in turn depend on (1) the *available supply of oxygen* in the water mass, with which the mud surface is potentially in contact by means of eddy diffusion, and (2) the *degree of eddy*

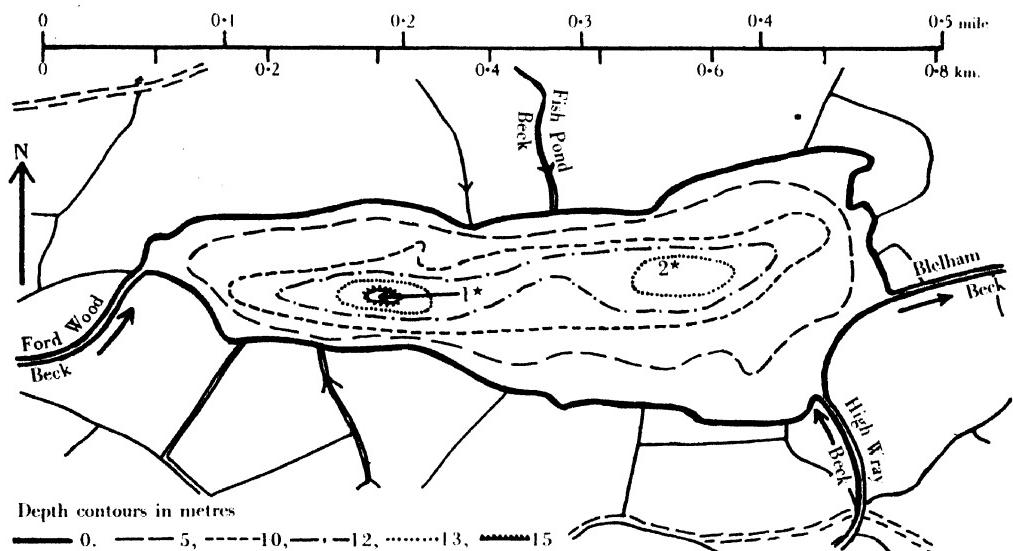


Fig. 40. Bathymetric map of Blelham Tarn. Contours from echo-sounding survey (Mortimer, in prep. VI). \* Sampling stations.

*diffusion* in this water mass. (1) also depends to some extent on the rate at which reduction processes occur in the water. It is possible to make certain deductions from this hypothesis and to apply *rough* checks with available data.

Deduction 1: If the mean thickness of the oxidized layer be compared in a series of lake muds during a period when the oxygen concentration at the mud surface is maintained at the same *constant level* in all cases, e.g. during the winter circulation period, each thickness will be in *inverse relation* to the oxygen-absorbing power of the respective mud. A rough comparison has been made, for a series of English Lake District lakes, between (a) the rate of oxygen absorption from the hypolimnion during summer thermal stratification, and (b) the approximate mean thickness of the oxidized layer during

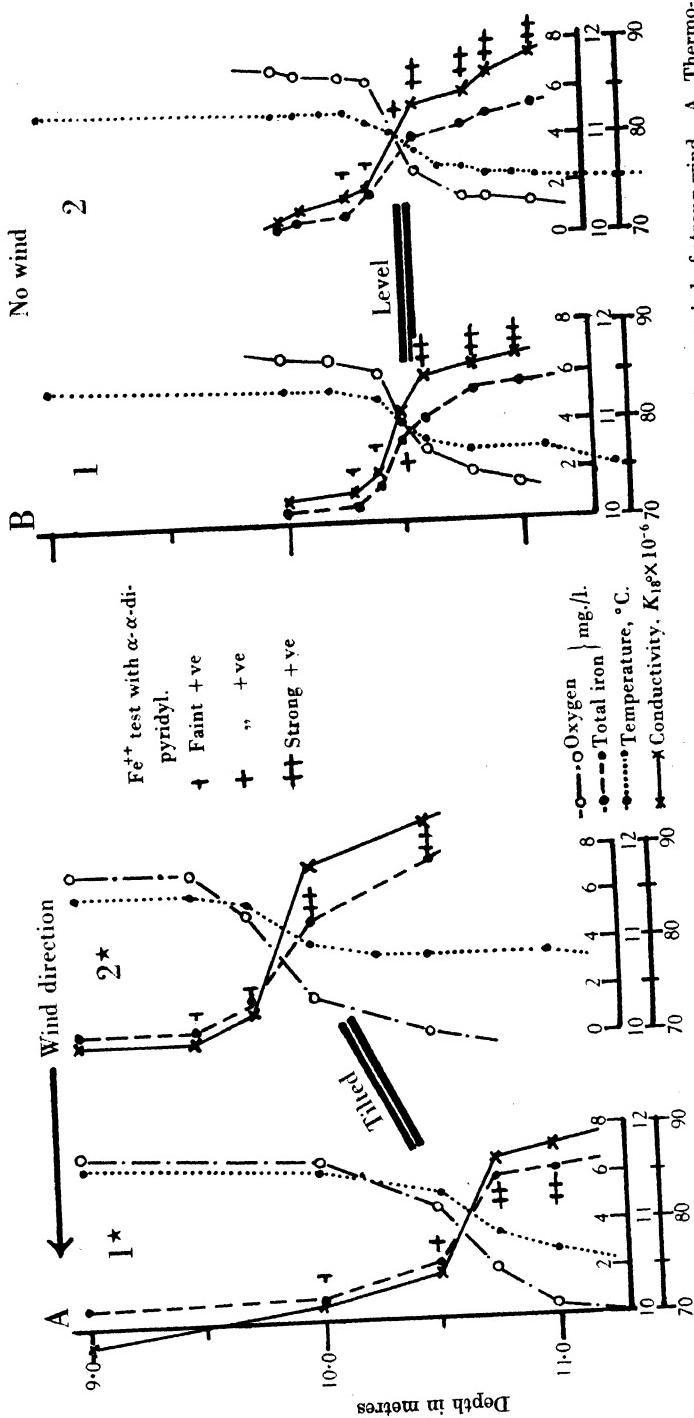


Fig. 41. Blelham Tarn. Development and decay of a thermocline tilted, 5 October 1939, 3.30 p.m. Strong continued east wind since 3 October; died down in gales on the morning of 7 October. \* For positions of sampling stations, see Fig. 40.

the period of winter circulation. This comparison is of value, not because the data can claim to be complete or more than approximately representative, but because it discloses interesting general relationships and indicates a possibly useful method in regional limnology.

(a) The approximate oxygen absorption rate of Esthwaite mud may be estimated by inspection of Fig. 13, § I. An approximation to the rate in four other Lake District lakes has been obtained from a knowledge of the extent of oxygen depletion in the hypolimnion at the end of the summer stagnation period. In Fig. 42 the observed oxygen concentration at each depth is plotted, as well as at that concentration which represents 93 % saturation under the same temperature conditions, this being the usual degree of saturation observed in these lakes during winter. No correction was made for the height of the lakes above sea-level. The difference between the observed and the 93 % saturation values represents the 'actual deficit' (see discussion in Hutchinson, 1938a), and has been employed in preference to Alsterberg's 'absolute deficit' (i.e. difference between observed concentration and the 100 % saturation value at 4° C.), as the use of the latter is theoretically unsound (Grote, 1936), although its employment may possess certain practical advantages (Hutchinson, 1938a). The total 'actual deficit' in the hypolimnion of each lake was determined planimetrically from Fig. 42. This, divided by the number of days between the date of observation and 1 May, on which date thermal stratification was assumed to have begun, yields a mean daily oxygen decrement for the whole water column, expressed as grams per sq. m. of mud surface per day in Table 5. This value is higher than the 'areal hypolimnetic oxygen deficit' of Hutchinson (1938a), but is not far removed from it. The values given in Table 5 are simpler to compute and are sufficient for this rough comparison of muds of widely differing oxygen-absorbing power. Values comparable to those of Hutchinson have been computed for Windermere, North and South Basins 1932, by P. M. Jenkin (unpublished data). Increments in 'areal hypolimnetic deficit' in both basins was found to vary about 0·4 g./m.<sup>2</sup>/day (personal communication). These values are not far different from those found in 1938–40.

(b) Estimates of the mean winter thickness of the oxidized layer, i.e. depth of the isovolt  $E_7=0\cdot20$  V. below the mud surface, were obtained by inspection of Fig. 43, which illustrates representative winter distribution of potential in cores from deep regions of five lakes in the English Lake District. These estimates are entered in Table 5. That given for Crummock Water is probably too low, as only a summer observation was available. However, this lake has been included as it occupies an intermediate position between oligotrophic Ennerdale and mesotrophic Windermere (definitions later).

Stating deduction (1) more precisely: If it is assumed (i) that, in any one lake, the summer and winter oxygen absorption rates are roughly proportional, and (ii) that in all lakes the winter oxygen concentration ( $C_w$ ) at the

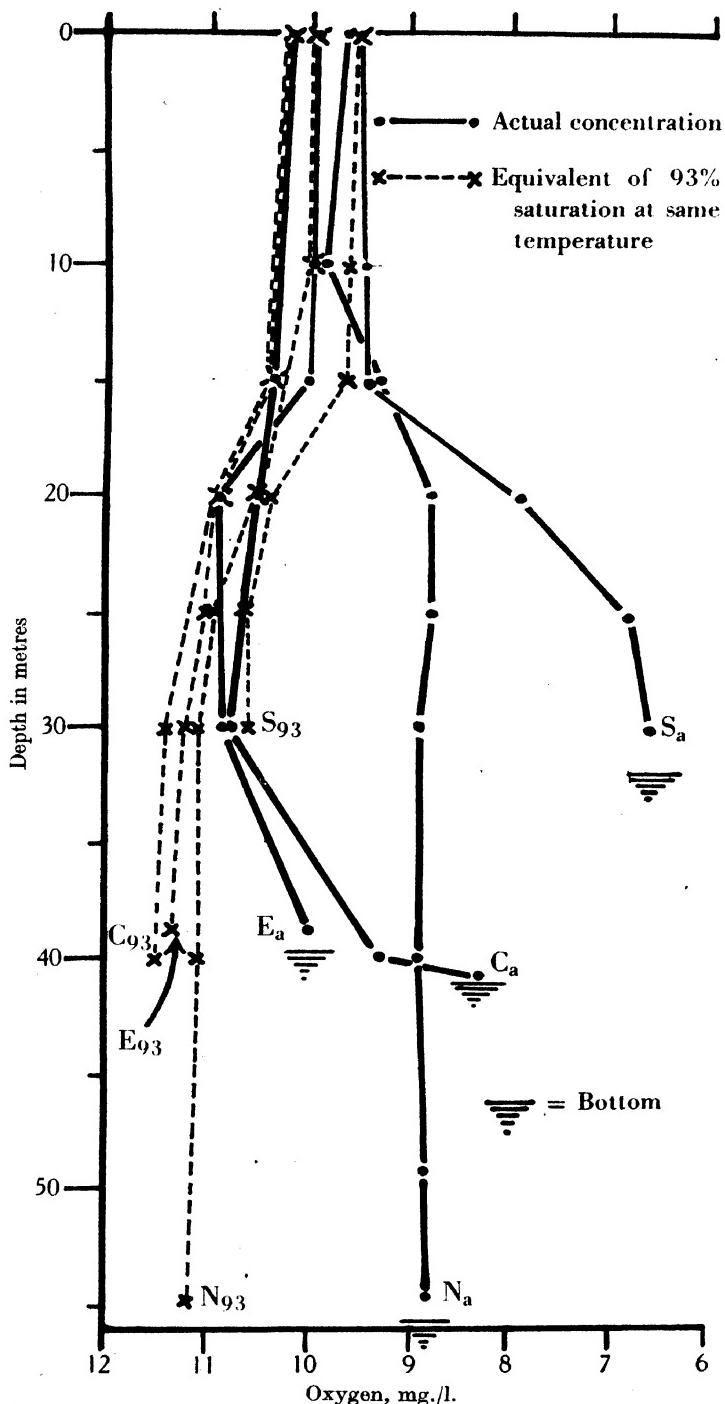


Fig. 42. Comparison, in various lakes, of (i) the depth distribution of dissolved oxygen at the end of summer stagnation with (ii) that representing 93% saturation under the same temperature conditions. Ennerdale Water (E), 17 August 1940. Crummock Water (C), 3 September 1940. Windermere, South Basin (S), 4 October 1939. Windermere, North Basin (N), 11 October 1939. Suffix *a* equals 'actual concentration'; suffix '93' equals '93% saturation value'.

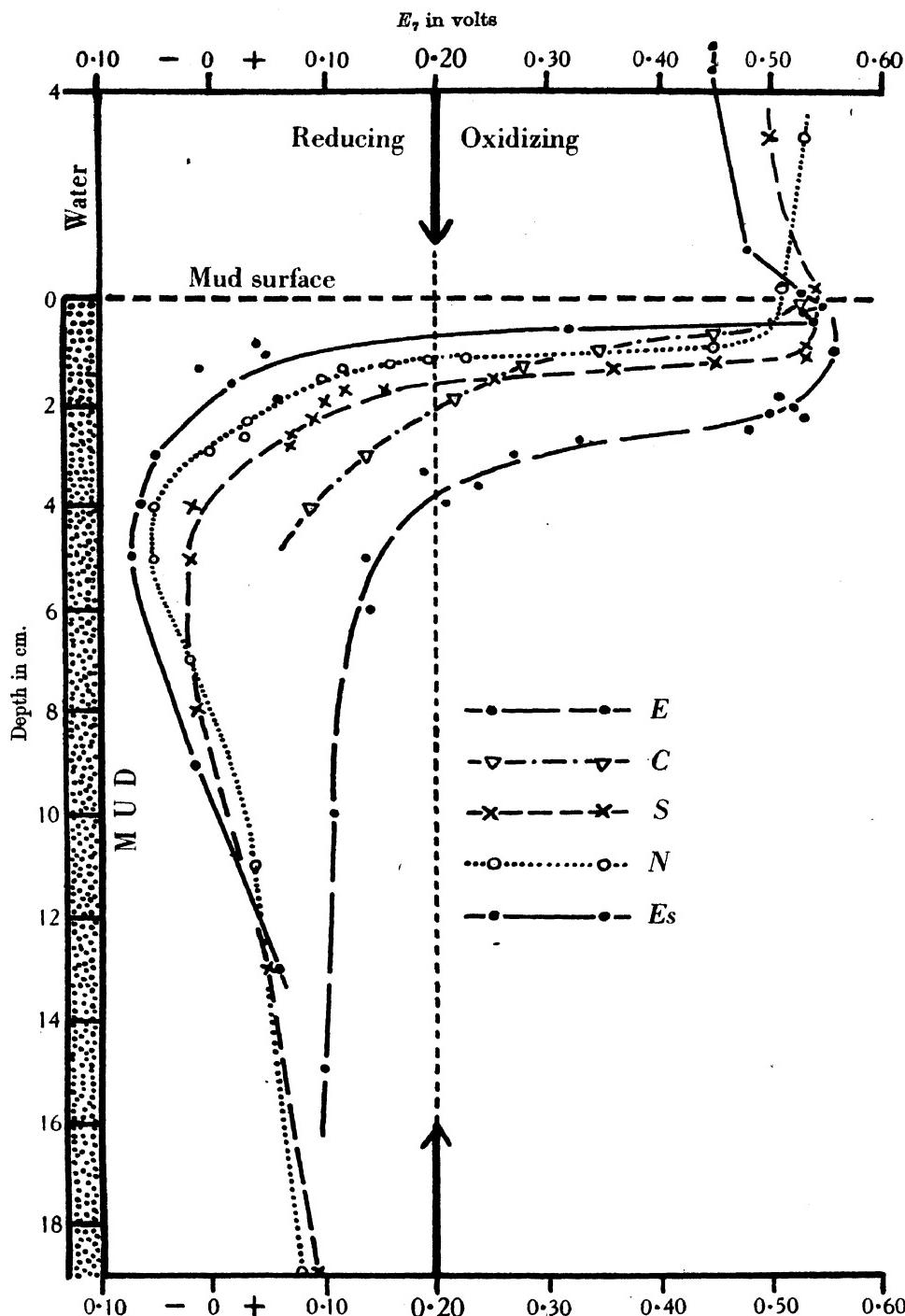


Fig. 43. Typical winter distribution of redox potential ( $E$ , in volts) in the surface mud cores from the deep regions of various lakes. Ennerdale Water (E), 40 m., 5 March 1941. Crummock Water (C), 40.8 m., 3 September 1940 (N.B. single summer observation). Windermere, South Basin (S), 31 m., 11 February 1941. Windermere, North Basin (N), 65 m., 6 February 1941. Esthwaite Water (Es), 14 m., 12 March 1941.

mud surface, and also the coefficient of diffusion ( $k$ ) in the mud is of the same order, then the following relationship should be found:

$$\text{Summer oxygen absorption rate } (O) \propto \frac{kC_w}{\text{thickness oxidized layer } (T)}.$$

Thus if  $(O)$  is plotted against  $(T)$ , the points should lie on a rectangular hyperbola, i.e. if  $\log(O)$  is plotted against  $\log(T)$ , the points should lie on a straight line. For the data given in Table 5 this is found to be approximately the case (Fig. 44 A).

Table 5. Comparison of (a) estimates of the oxygen absorption with (b), winter thickness of the oxidized layer, (c) redox potential at 5 cm. depth, and (d) organic content of muds from the deep regions of various lakes

Lake	...	Ennerdale Water (E)	Crummock Water (C)	Windermere		Esthwaite Water (Es)
				South Basin (S)	North Basin (N)	
Max. depth, m.*		43.9	43.9	44	67	16
<b>I. Estimate of (a) mean daily increment (<math>O</math>) of 'actual oxygen deficit', in hypolimnion water column (g./sq. m. mud surface)</b>						
Date of observation	17. viii. 40	3. ix. 40	4. x. 39	11. x. 39	Mean May-July cf. Fig. 13	
Limits of Water column, m.	15-39.8	15-40.8	15-31	Off Lowood 15-55		9-14
$O$ , g./m. <sup>2</sup> /day	0.09	0.16	0.31	0.52		0.65
<b>II. Estimate of (b) winter thickness (<math>T</math>) of oxidized surface mud layer and (c) mean winter redox potential (<math>E_7</math>) at 5 cm. depth</b>						
Date of collection	5. iii. 41	3. ix. 40†	11. ii. 41	6. ii. 41	12. iii. 41	
Water depth, m.	40	40.8	31	65‡		14
$T$ , cm.	4.0	2.2	1.7	1.1		0.7
$E_7$ at 5 cm. (V.)	+0.14	+0.06	+0.02§	-0.05		-0.07
<b>III. (d) Organic content of Petersen grab samples (Misra, 1938)</b>						
Water depth, m.	40			50		12
Loss on ignition, % dry wt.	12.84			16.84		21.34
Total N, % dry wt.	0.4506			0.5384		0.8539

\* Other morphometric data in Mill (1898).

† N.B. summer value.

‡ Only case in this series in which mud samples taken at a point removed from that at which O<sub>2</sub> depletion was estimated.

§ Mean of 24 cores; higher value than indicated in Fig. 43.

Hutchinson (1938a) has demonstrated that, in a series of geographically separated and morphologically different lakes, the increment of 'areal hypolimnetic deficit' is proportional to plankton production in each lake. He has suggested the limits  $H-H$  (Fig. 44 A) for mesotrophic lakes. All lakes with increments above or below these limits are classed as eutrophic or oligotrophic respectively. Thus, even allowing for the difference between Hutchinson's

'areal deficit' and ( $O$ ) (Table 5), Hutchinson would class Windermere, North Basin and Esthwaite Water as eutrophic and Windermere, South Basin, and Crummock Water as mesotrophic. It may be suggested, as a matter of opinion, that the limits  $L-L$  (Fig. 44 A) fit the observed conditions in the English Lake District better. Thus Ennerdale Water and Crummock Water are considered to be oligotrophic and Esthwaite Water to be eutrophic.

Fig. 43 illustrates differences in the distribution and general level of redox potential in the muds of the lakes. These differences are expressed, not only in the thickness of the oxidized layer, but also in the value of the minimum redox potential in the core, usually to be found at about 5 cm. below the surface. This minimum, and the gradual rise in potential with increasing depth below 5 cm., may indicate more intense anaerobic organic decomposition at

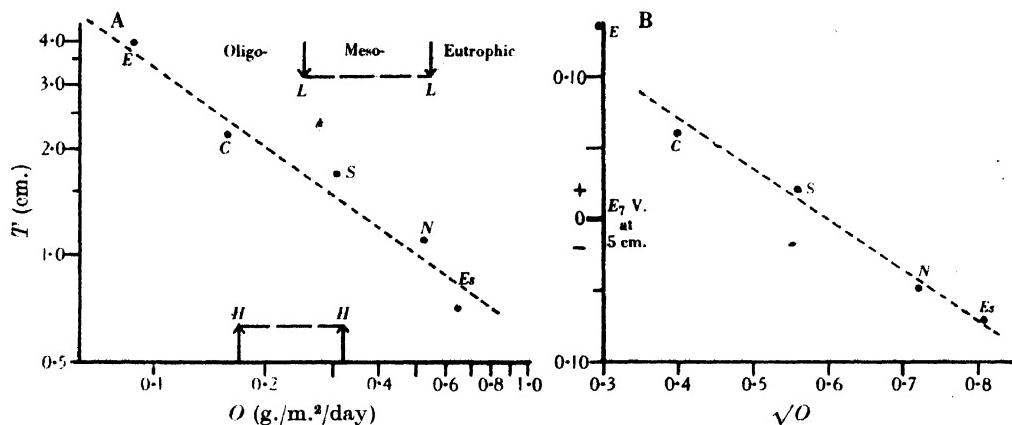


Fig. 44. Correlations (A) between the rate of oxygen absorption  $O$  and the winter thickness of the oxidized surface mud layer  $T$ , and (B) between the winter redox potential ( $E_7$  in volts) at 5 cm. depth in the mud and  $\sqrt{O}$  in muds from deepest regions of various lakes. Abbreviations as in Fig. 43.

the 5 cm. level, i.e. just below the oxidized layer, and a decrease in intensity in older and lower deposit. ZoBell (1937) recognizes that the oxygen-absorbing power ( $O$ ) of muds is the product of an *intensity* ( $I$ ) and a *capacity factor* ( $K$ ), i.e.  $O=I \times K$ . If redox potential is equated to  $I$ , it is possible to envisage a mud of low potential, i.e. high intensity ( $I$ ), but with low oxygen-absorbing capacity ( $K$ ), and vice versa. If, on the other hand,  $I$  is proportional to  $K$ ,  $I$  will be proportional to the square root of the oxygen-absorbing power. This holds (Fig. 44 B) roughly for the muds investigated.

A similar, although less detailed, observation of a redox potential minimum just below the mud surface was made by Karsinkin *et al.* (1930). These workers were the first to publish results of measurements of potentials in muds and to point out their relation to redox conditions in the water. Since then other measurements have been made by the same authors (1931), by Iwlew (1937)

in connexion with a detailed study of season changes in distribution of various forms of iron in mud and water, and by Misra (1938).

In non-peaty muds it might be expected that organic content is the most important factor determining the level of redox potential. Unfortunately, data for Lake District muds are insufficient to test this: However, if loss on ignition and total N values of muds from the same localities (Misra, 1938) are compared with  $E_7$  at 5 cm. (Table 5), the muds are seen to fall into the same order if arranged according to organic content or potential.

Typical winter distribution of electrical conductivity in the surface mud in the deepest regions of the same five lakes is illustrated in Fig. 45. Comparison of this with Figs. 42 and 43 demonstrates another correlation, namely, that between oxygen-absorbing power and electrical conductivity. The highest conductivity and also the most rapid increase of conductivity with depth is found in the muds with the highest rate of oxygen absorption and lowest potential. The depth distribution of conductivity is approximately exponential. Thus, if the log of the slope of the conductivity curves in Fig. 45 is plotted against depth, the points over a large part of the curve lie approximately on straight lines (Fig. 46 A). Deviations from this line at the mud surface indicate adsorption of ions in the oxidized layer. Other deviations, usually found at about 12 cm. depth, may indicate changes in the rate of production of ions at these levels. A mathematical analysis of these and similar curves will be attempted in a later publication (Mortimer, in prep. I). The following empirical relation, however, may be noted here. The squares of the slopes ( $S$ ) of the lines in Fig. 46 A are roughly proportional to ( $O$ ) (see Fig. 46 B). If we assume with Grote (1934, p. 33) that the rate at which oxygen is utilized in decomposition is a measure of the rate at which mineral substances are liberated, and of the rate of lake 'metabolism' as a whole, the above empirical relation suggests a formula of the following general type, which gives the conductivity ( $K$ ) at depth ( $z$ ) in the mud:

$$K_z = K_L + (K_O - K_L) e^{-z\sqrt{(r/c)}},$$

where  $r$  is the rate of production of ions in the mud,  $c$  is a constant which includes the coefficient of diffusion in the mud,  $K_O$  equals the conductivity at the mud surface, and  $K_L$  is the limiting value of  $K$  which is approached with increasing depth. Deviations from this theoretical distribution may indicate variation in  $c$  or (more likely) in  $r$ . The above formula is of the same general type as that which expresses the distribution of the steady state of temperature along a long bar, heated at one end and losing heat by radiation and conduction all along its surface (Carslaw, 1921).

A second deduction may be made from the original hypothesis (p. 180). Assuming the oxygen-absorbing power of the mud to remain constant, and neglecting any lag due to the slowness of reduction of oxidized compounds (e.g. ferric hydroxide), the thickness of the oxidized layer in any one mud

will be directly proportional to the oxygen concentration at the mud surface. The data are insufficient to check this.

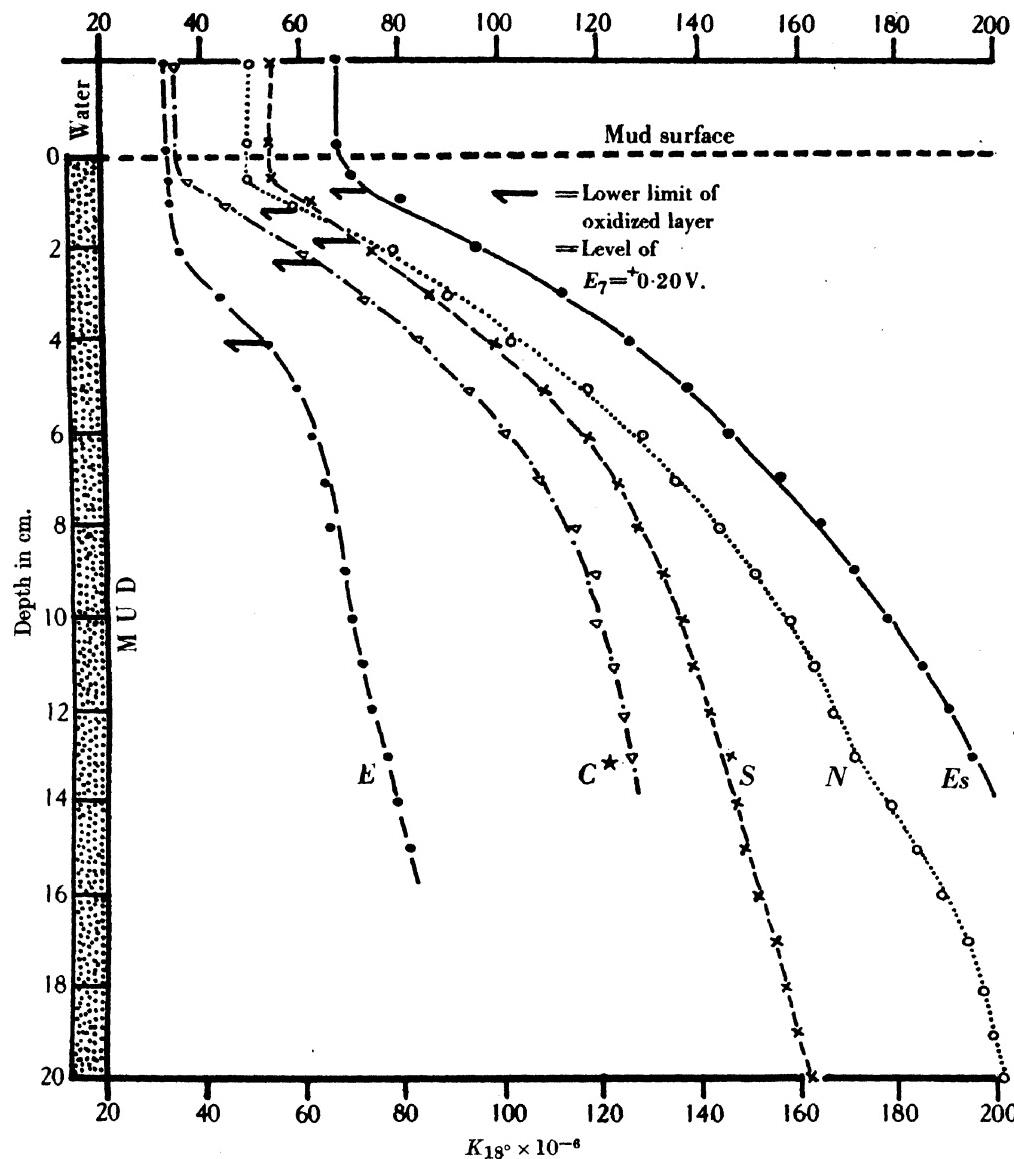


Fig. 45. Mean winter distribution of electrical conductivity ( $K_{18^\circ} \times 10^{-6}$ ) in the surface mud cores from deepest regions of various lakes. Abbreviations and depths as in Fig. 43.  
 \* Single summer observation.

A third deduction, which has a bearing on productivity problems, is as follows. In lakes with muds of approximately equal oxygen-absorbing power, depletion of oxygen in the hypolimnion—for which in most cases the mud is mainly responsible—may appear either as a small 'volume-deficit' in

a deep lake or as a large 'volume-deficit' in a shallow lake (cf. Hutchinson, 1938a and refs. there). The mud surface will only become reduced and exhibit the accelerated liberation of ions from the mud associated with this, in lakes sufficiently shallow to produce a large enough 'volume-deficit' at the mud surface. In shallow lakes the volume of the hypolimnion is probably the main controlling factor, for, as this must be considered as a partially closed system, the total available supply of oxygen is limited. In lakes of medium and greater

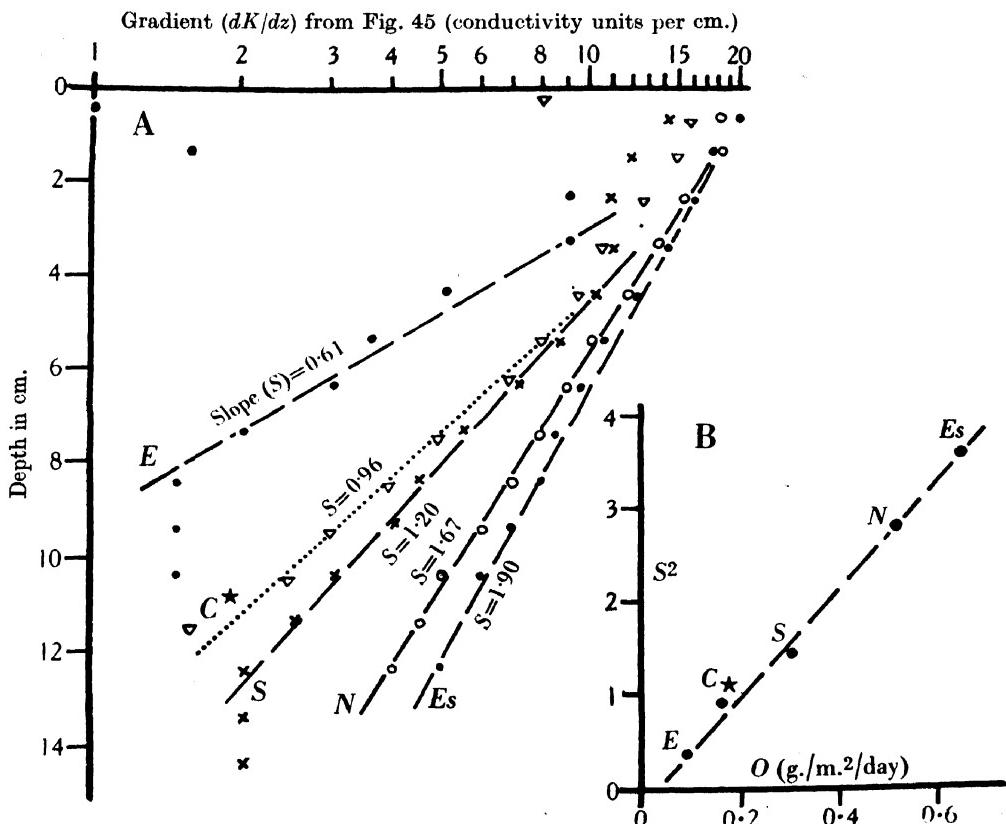


Fig. 46. A. Logarithms of the gradients of curves in Fig. 45 (i.e.  $\log dK/dz$ ) plotted against depth ( $z$ ). B. Comparison of the slopes ( $S$ ) in Fig. 46 A with the rate of oxygen absorption ( $O$ ) of the mud. Abbreviations as in Fig. 43. \* Single summer observation.

depths the volume of the hypolimnion becomes of less importance relative to the degree of eddy diffusion, which apparently increases with depth and other morphometric factors (Table 4). If this were not so—i.e. if the degree of eddy diffusion were to remain the same in all lakes, both deep and shallow, with muds of the same oxygen absorbing power—the vertical distribution of oxygen relative to the mud surface would be identical in *all* lakes of more than a certain depth. No mechanism would exist whereby a greater depth of hypolimnion could exert its influence. A study of chemical stratification in deep

lakes during summer thermal stratification and comparison of this with stratification developed under ice, where eddy diffusion may be expected to be low, should yield data to check the above conclusions.

*Classification of lakes.* Before proceeding to discuss the possible effect of redox conditions at the mud surface on productivity, it is necessary to outline certain ambiguities which have arisen in the classification of lakes on a productivity basis. The original and perhaps the clearest definition (refs. in Naumann, 1932) depended entirely on the degree of plant production and the edaphic (geochemical) factors which control this. Subsequently, other features, often but not necessarily associated with oligotrophic or eutrophic conditions, have been employed to class lakes into *oligotrophic*, *eutrophic* or intermediate (*mesotrophic*) categories. Thus a high or low degree of de-oxygenation in the hypolimnion has been termed a eutrophic or oligotrophic condition respectively (Thienemann, 1928), because in the majority of cases these features have been found to be associated with a high or low degree of organic production. Emphasis is thus laid more upon the oxygen conditions—possibly of greater interest to the zoologist—than upon the degree of plant production, although unfortunately the same terminology is employed. Recognizing the influence of the shape and size of the basin on the distribution of oxygen, Thienemann (1928) has included the *morphometric factor* as one of the most important in determining the trophic condition of lakes, regarding it as *inseparable* from other factors (cf. p. 146). Lundbeck (1934), however, distinguishes between primary, *edaphic oligotrophy* on the one hand and secondary *morphometric oligotrophy* (great depth) on the other. The logical conclusion from this view has been stated by Hutchinson (1938a), who considers that the edaphic and morphometric determinants 'in great measure vary independently' (my italics), and that the influence of the latter may be eliminated in a comparison of the productivities of morphologically different lakes by the employment of the concept 'areal hypolimnetic oxygen deficit'.

The limitations of the latter concept, especially when applied to shallow lakes (cf. Riley, 1939, cit. Deevey, 1940), should not be ignored. With these limitations in mind, the concept may be applied with profit to the study of regional limnology in areas from which plankton data are not available. Hutchinson has pointed out that the close relation between 'areal deficit' and plankton production breaks down when considerable quantities of allochthonous organic matter are present. This suggests that a more general relation is one between (a) areal deficit and (b) reducing power of the mud. This may explain a discrepancy observed between the North and South Basins of Windermere. A study of plankton production in these two basins over a period of years has shown that phytoplankton production in the South Basin is at least double that in the North Basin; zooplankton production is also significantly higher in the former. The mud in the South Basin, however, is less reducing than in the North Basin (Fig. 43), and the oxygen deficit in the

hypolimnion (Fig. 42) in these two basins is correlated, not with the amount of plankton produced in the epilimnion, but with the reducing intensity of the mud. This is possibly controlled by the distribution of decomposing leaf fragments, which are found in considerable quantities in the mud of the North Basin, especially in regions near the larger inflows, but are relatively infrequent in the muds of the South Basin, which receives most of its inflow from the North Basin.

It is of interest to speculate what light is thrown on the above confusing, if not conflicting, views of lake classification by the demonstration, in previous sections, of the acceleration in liberation of ions, including many plant nutrients, during reduction of the mud surface. As the resulting increase in concentration of solutes in the water is large, this event may be considered to have a profound influence on the degree of organic production in the water. It has been shown that, in all but exceptionally reducing muds, this event can only occur in relatively shallow lakes. Extreme oligotrophy, on the other hand (primary oligotrophy in Lundbeck's sense), will not be associated with oxygen exhaustion, even in lakes with the small hypolimnia. A causal connexion may therefore be expected, in the higher ranges of productivity only, between degree of organic production and depth of lake. If this connexion can be demonstrated by extended studies of regional limnology, it lends support to the general observation at the basis of Thienemann's views that high production is more often than not associated with a high degree of oxygen depletion in relatively shallow lakes, and that morphometric and edaphic determinants of production are not entirely independent. It was emphasized earlier that the morphometric determinant includes not only dimensional factors, but also the influence of these on water movements and the degree of eddy diffusion, which clearly also depends on climate. These speculations can only be tested by future work. The present position has been summed up by Rawson (1939, cit. Deevey, 1940): 'while the edaphic factors determine the kinds and amounts of primary nutritive materials, the morphology of the basin and the climate may to a large extent determine the utilization of these materials'.

*Lake evolution.* It is also of interest to suggest briefly how the above speculations may apply to the concept of lake evolution. Any change in the productivity of the water may be expected to produce a change in the organic content and reducing power of the mud. If an increase in productivity, not necessarily uniform or continuous, is an evolutionary tendency, and the lake is sufficiently shallow, a point in time will be reached at which the mud surface becomes reduced. This will have the effect, noted in Esthwaite Water, of accelerating (a) oxygen depletion in the hypolimnion, and (b) the release of ions from mud to water. Thus a primary phase (I) of slow increase in productivity may be expected to be followed by a secondary phase (II) of accelerated increase, in which, under reducing conditions, the adsorbing influence

of oxidized ferric complexes is destroyed, resulting in liberation and a more complete utilization of plant nutrients. Further reduction, resulting from this accelerated increase in production of organic matter, may induce a tertiary highly reduced sterile phase (III), in which in many cases the iron is again precipitated as sulphide. The rate at which these changes take place will be determined by geochemical and morphometric factors. Very deep lakes and all geochemically oligotrophic lakes may never pass out of the phase I, before they become silted up. Shallow and highly eutrophic lakes may pass through all three stages in a very short time after their formation, or they may become arrested in phases I or II (cf. 'trophic equilibrium' in Linsley Pond, Hutchinson & Wollack, 1940), because the 'sterility' of the mud, associated with the phase III, has not sufficient depressing influence on production as long as ample nutrient supplies are continuously available from the drainage area. Further change will be caused only by variation (e.g. cultural) in this rate of supply. This suggests that changes or lack of change in lakes is determined mainly by the individual characters of lake basin and drainage area, as well as climate. The greatest rate of change is probably at the end of phase I, and we may expect to observe this at the present day in mesotrophic lakes of moderate depths, or in lakes in which edaphic determinants are being changed by cultural influences. Examples of the former class are those lakes investigated by Ohle (1933-4), in the course of an extensive chemical survey of north German lakes, in which oxygen depletion in the hypolimnion has considerably increased in recent years ('Eutrophierung'). The best example of the latter class is afforded by Lake Zürich (Minder, 1938), in which the sudden acceleration of oxygen depletion and plankton productivity, as a result of sewage pollution, is recorded in detail in the deposits.

#### SUMMARY

This study of physical-chemical aspects of organic production in lakes is concerned (*a*), in general, with investigation of factors operating in the lake system (water + deposits) to control the rate of supply of nutrients to the phytoplankton, and (*b*), in particular, with seasonal changes in the hypolimnion and bottom mud, and with mechanisms controlling the release of nutrients to the water. The investigation developed in three stages: (1) study of distribution of physical properties and solutes in a lake subject to wide seasonal fluctuations in redox conditions; (2) laboratory experiments on mud-water systems; (3) correlation, in oligo- and eutrophic lake types, of seasonal changes in water and mud. A fourth section, 'General Discussion', is added, in which a hypothesis of chemical exchange between mud and water is outlined, and its application to limnological theory discussed.

§ I. Samples were obtained at approximately weekly intervals from April 1939 to February 1940 at 1, 5, 6, 7, 8, 9, 10, 11, 12 and 13 m. depth at a sampling station (14 m. depth) in the deepest region of Esthwaite Water. The

following determinations were made on these samples by standard methods: temperature,  $O_2$ , alkalinity,  $pH$ ,  $NH_4^+$ ,  $NO_2^-$ ,  $NO_3^-$ , Si, P,  $Fe^{+++}$ ,  $Fe^{++}$ , total Fe, and  $S^{--}$ . New methods are described for the estimation of conductivity, redox potential (corrected to  $E_7$ , i.e.  $E_h$  at  $pH\ 7.00$ ),  $SO_4^{--}$ , turbidity and colour.

Seasonal variation in stratification of each property is illustrated in a series of 'depth-time diagrams' (Figs. 3-10), which demonstrate correlations between weather (Fig. 2) and thermal and chemical stratification.

Events in the hypolimnion after the onset of thermal stratification were as follows:

Stage I (June to mid-July). The rate of oxygen depletion was greater with increasing depth; the mean rate in the whole hypolimnion was at first fairly constant, but was retarded later when the concentration in the bottom sample had fallen to 2 mg./l. Increases in alkalinity, conductivity, colour and iron content were observed.

Stage II (mid-July to mid-August) was initiated by a rapid fall in redox potential and oxygen concentration in the bottom sample to  $E_7$ , 0.25 V. and 0.5 mg./l. respectively. This was followed (Fig. 12) by a rapid rise (greater with increasing depth) of alkalinity, conductivity, Fe, Si, P, colour and turbidity, accompanied by decrease of  $NO_3^-$  and the appearance of relatively large amounts of  $NO_2^-$  at certain levels. Increase in turbidity and colour resulted mainly from the oxidation and precipitation as  $Fe(OH)_3$  of considerable quantities of  $Fe^{++}$  appearing at the mud surface at this stage. This accounted for an accelerated decrease in  $O_2$  concentration, which at lower levels became zero (unmodified Winkler estimation), by which time  $Fe^{++}$  was detected in the water and the potential had fallen to  $E_7$ , 0.15 V. From this point onwards the Fe content of the hypolimnion increased rapidly and an increasing proportion consisted of  $Fe^{++}$ .

Rapid ammonia production, at this stage, was of greater magnitude than the equivalent of nitrate reduction, which by then was complete at lower levels (Fig. 13). Nitrogen relationships indicate that, under oxidizing conditions, nitrification occurs most actively in the oxidized mud surface, and that, under reducing conditions, the mud is the main source of ammonia.

Stage III (mid-August and September) exhibited a continued but slower rate of rise in concentration of solutes. The hypolimnion became less turbid, but colour due to organic matter persisted.

The overturn (5 October), preceded by an encroachment into the hypolimnion by a progressive fall in level of the thermocline, resulted in rapid reversal of the above reduction changes. An immediate rise in  $O_2$  content was followed by a rapid fall in alkalinity, conductivity, Fe, Si, P and  $NH_4^+$ . Colour fell off less rapidly, and  $NO_3^-$  began to increase some weeks later.

From computations of the total amount of certain solutes, assumed to have been derived wholly from the mud, which passed upwards through

selected levels in the hypolimnion water column, and from the respective concentration gradients at those levels, it was possible to estimate roughly the mean eddy diffusion coefficient for selected periods. The estimates ( $3 \times 10^{-2}$  c.g.s. units, Table 1) are approximately 20 and 2000 times the respective molecular coefficients of heat conduction and chemical diffusion.

During 7 weeks under ice cover, changes were observed in Esthwaite Water and Blelham Tarn similar to, but slower than, those described for stage I. The eddy diffusion coefficient (Table 2) was estimated at one-sixth of that during stage I. Even so, it was more than 200 times the molecular coefficient, indicating that convection currents prevent complete stagnation under ice. 94% of dissolved salt content, all humus colouring matter and a large part of dissolved gas content were removed from the water on freezing (Table 3). This led to increases in concentration in the water immediately under the ice.

Large-scale seasonal changes in dissolved salt content of the hypolimnion were confined to the group of solutes producing alkalinity (Fig. 14). Only part of the alkalinity increase could be accounted for by increase in  $\text{NH}_4^+$  and Fe. That portion due to other bases exhibited a slow increase during stage I, a rapid increase during stage II, remained at a constant level during stage III (although  $\text{NH}_4^+$  and Fe continued to increase), and fell gradually after the overturn.

Until stage II, a surface-oxidized mud layer of a few millimetres depth could be recognized by the presence of precipitates of  $\text{Fe(OH)}_3$  and associated complexes. Much of this material was in colloidal form and possessed adsorbent properties. Fe below this layer was in soluble ferrous state. Changes observed at the beginning of stage II suggest that, below a limiting  $\text{O}_2$  concentration and redox potential, colloidal ferric precipitates in the mud surface were reduced, resulting in the liberation of (i) adsorbed bases, and (ii)  $\text{Fe}^{++}$ . The rate of spread of the latter was considerably increased by the transition from molecular diffusion in the mud to turbulent diffusion in the water, accounting for the accelerated rate of oxygen depletion. With the removal of the adsorbent barrier constituted by the oxidized mud surface, exchange of solutes between mud and water was relatively unimpeded (stage III). The process was reversed at the overturn. Gradual fall in alkalinity during subsequent months may be attributed to selective adsorption of bases by the reconstituted oxidized mud surface.

Many of the events described in Esthwaite Water were demonstrated in Schleinsee (Fig. 15) using published data of Einsele & Vetter (1938).

§ II. In laboratory experiments designed to test the above hypothesis, artificial mud-water systems were subjected to the following treatments: (1) artificial aeration, (2) water surface exposed to air, (3) water surface sealed from air by liquid and solid paraffin. Equipment is described for sampling,  $\text{CO}_2$  estimation, pH and conductivity determinations in mud, and measurement of redox potential at 2 mm. depth intervals above and below

the mud surface. Measurements in the mud and estimations in the water (those listed in § I, with  $\text{CO}_2$  and Mn in addition) were made over a period of 152 days.

Results are presented in depth-time diagrams of redox potential and conductivity in the mud (Fig. 18) and graphs of concentration of solutes in the water, uncorrected for change of volume on sampling (Figs. 19, 20).

Changes in 'aerated' tanks (1 and 2) were practically identical, although more rapid in the former. The water retained the characters of oxygenated lake water and, apart from a fall in  $\text{NO}_3^-$  and alkalinity and a rise in Si and  $\text{SO}_4^{--}$ , little variation in concentration of other solutes or in mud conductivity occurred. The oxidized surface mud layer, bounded by the isovolt  $E_7$ , 0.24 V., gradually increased in thickness. The fall in nitrate and alkalinity is attributed to the high mud/water volume ratio and the adsorbent effect of the oxidized mud surface, respectively.

Changes of much greater magnitude were observed in the 'anaerobic' tank (3). After effective sealing from the atmosphere, a fall in  $\text{O}_2$  and  $\text{NO}_3^-$  and a rise in  $\text{CO}_2$ ,  $\text{NO}_2^-$  and  $\text{NH}_4^+$  concentrations commenced. The oxidized surface mud layer became progressively thinner, disappearing after a period of 40 days, at which time the isovolt  $E_7$ , 0.24 V. rose into the water. From this point onwards, similar changes to those in stage II, § I, were observed, i.e. considerable increases in alkalinity, conductivity, Fe, Mn and turbidity, followed by the appearance of  $\text{Fe}^{++}$  and the rapid increase of Si, P, colour and mud conductivity, and accelerated decrease in  $\text{SO}_4^{--}$ . By this time only traces of oxygen remained (Alsterberg's modification of Winkler's method);  $\text{NO}_3^-$  and  $\text{NO}_2^-$  had disappeared.  $\text{SO}_4^{--}$  became completely reduced at a later stage, during which a decrease in Fe content of the water and of conductivity in the mud was attributed to precipitation of ferrous sulphide.

A list of approximate redox potential ranges ( $E_7$ , V.), within which the following reductions proceeded actively, is appended. The lower potential is the limit below which none of the oxidized phase could be detected.  $\text{NO}_3^-$  to  $\text{NO}_2^-$ , 0.45–0.40;  $\text{NO}_2^-$  to  $\text{NH}_4^{++}$ , 0.40–0.35; ferric complex to ferrous complex or  $\text{Fe}^{++}$ , 0.30–0.20;  $\text{SO}_4^{--}$  to  $\text{S}^{--}$ , 0.10–0.06. The  $\text{O}_2$  concentrations associated with these ranges were 4, 0.4, 0.1 and zero mg./l., respectively.

§ III. The chemical survey described in § I was repeated for a further annual cycle on Esthwaite Water, also in less detail on Blelham Tarn, and extended (for comparison with lakes in which de-oxygenation of the hypolimnion does not occur) to Windermere, North and South Basins. At less frequent occasions other lakes in the English Lake District were investigated. The following estimates were made, in addition to those listed in § I:  $\text{O}_2$  by Alsterberg's modification of Winkler's method,  $\text{CO}_2$ , Mn and Cl. Concurrently, techniques described in § II were applied to the study of the distribution of redox potential, pH and conductivity in undisturbed cores of mud, and water in contact with it, obtained with a new type of sampling apparatus (Fig. 22).

Results from (A) Esthwaite Water and (B) Windermere, North Basin, have been selected as representative of two fundamentally different lake types.

(A) Events in the hypolimnion were almost identical with those described in § I, while concurrent changes in the mud and their correlation with changes in the water closely resembled those observed in the 'anaerobic' tank, § II. The oxidized surface mud layer, bounded by the isovolt  $E_7$ , 0·20 V.; was progressively reduced in thickness from 7 mm. on 9 May to zero on 12 June (Fig. 28).

This initiated stage II with accelerated rates of oxygen depletion and increase of alkalinity, conductivity, Fe,  $\text{NH}_4^{++}$ , Si and turbidity in the water (Fig. 29), and rise in conductivity in the mud (Fig. 30). After the  $\text{O}_2$  concentration at the mud surface had fallen below 1·0 mg./l. (18 July), the isovolt  $E_7$ , 0·20 V. and  $\text{Fe}^{++}$  began to rise into the water. An explanation of the high conductivity below the mud surface at this time is not apparent. Presence of soluble  $\text{Mn}^{++}$  salts in the water prior to the appearance of  $\text{Fe}^{++}$  indicates that manganic precipitates in the oxidized mud surface are reduced at a higher potential than the ferric compounds.

Stage III exhibited, as in § I, a continued increase in concentration of certain solutes, and a steady decrease in potential in the mud surface and in the water just above, also a steady decrease in conductivity in the mud surface, probably due to ferrous sulphide precipitation. In the water  $\text{SO}_4^{--}$  was only reduced to half its original concentration; the potential only fell below that value ( $E_7$ , 0·10 V.), at which active  $\text{SO}_4^{--}$  reduction was observed in § II, for 2 weeks preceding the overturn.

There was no evidence of any considerable anaerobic production of  $\text{CO}_2$ .

Changes observed in the water at and after the overturn in § I were repeated. The oxidized surface mud layer was not re-established to spring thickness until over a month after the overturn, and was thereafter subject to considerable fluctuations, becoming thinner during the period under ice cover. This suggests that accumulated products of reduction in the mud surface (e.g. ferrous sulphide) were only slowly oxidized. Mud conductivity fell after the overturn, exhibiting some fluctuations and an increase under ice.

(B) The investigation of Windermere, North Basin, covered 3 months before and after the overturn. Changes in concentration of solutes above the mud (Fig. 31) at the overturn were definite but slight compared with those observed in (A). The thickness of the oxidized surface mud layer, i.e. depth of isovolt  $E_7$ , 0·20 V., was increased from 6 to 12 mm. (Fig. 32), and a decrease in mud conductivity was also observed (Fig. 33). This was confirmed by comparison (Figs. 34, 35) of conductivity in a number of mud cores from the deep region, examined before and after the overturn. Seasonal change in mud conductivity was greatest at 1·5 cm. below the surface, and was probably regulated by turbulence in the water just over the mud, and the thickness and adsorbent capacity of the surface oxidized layer.

The main difference between lakes of Esthwaite (A) and Windermere (B) type is that, in the latter, the  $O_2$  concentration in the water over the mud is not sufficiently depleted during thermal stratification to allow the adsorbent surface oxidized layer to be reduced and destroyed. Hence the considerable increase in rate of exchange of solutes from mud to water, initiated in type (A) by this destruction, is absent in type (B).

§ IV. Discussion is devoted in particular to the controlling influence on lake 'metabolism' of (i) water movements and (ii) processes in the mud, especially at the mud surface. The relation of (ii) to the ecology of profundal mud fauna is briefly discussed.

Evidence of (i) in the hypolimnion is indirect. Chemical surveys demonstrate that flow in the hypolimnion is largely horizontal, and permit the expectation that turbulence associated with this flow is the main exchange mechanism of heat and solutes. But, in order to account for observed distributions of these properties in the lower hypolimnion, it must be assumed that either (a) the eddy diffusion coefficient varies with depth, or (b) a non-turbulent exchange mechanism is operative. Examination of Hutchinson's evidence for (b) resulted in a provisional conclusion that (a) is more probable in large bodies of water.

It is suggested that wind-generated displacements of isosteres (cf. temperature seiches) can induce horizontal oscillatory water movements of sufficient magnitude in the hypolimnion to produce the observed degree of turbulence. Evidence of wind-induced tilting of isotherms and isopleths is presented (Figs. 37, 38, 39, 41). It is shown for eleven lakes that the degree of turbulence in the hypolimnion is proportional to depth and area (Fig. 36).

Investigation of seasonal changes in a central water column and underlying mud in five English Lakes disclosed relationships between the following: (i) winter  $O_2$  concentration ( $C_W$ ) above the mud surface, (ii) mean winter thickness ( $T$ ) of surface-oxidized mud layer (Fig. 43), (iii) winter reducing intensity ( $I$ ) of mud, measured by  $E_7$  at 5 cm. depth, (iv) winter conductivity in mud, (v) organic content of mud, and (vi) mean summer  $O_2$  depletion rate ( $O$ ) in hypolimnion, expressed per unit area of mud surface. It follows that  $C_W/T$ , i.e. the mean winter  $O_2$  concentration gradient maintained in the mud surface, is a measure of the reducing power of the mud. This was proportional to  $O$  (Fig. 44 A), and may be considered to be made up of intensity ( $I$ ) and capacity factors. These factors were not found to vary independently, for (I) was roughly proportional to  $\sqrt{O}$  (Fig. 44 B). (iii), (iv) and (v) exhibited rough proportionality. Increase in conductivity with depth in the mud was exponential, and an empirical relation between the exponent and  $\sqrt{O}$  was found (Fig. 46).

Reduction of the mud surface and the associated increase in supply of solutes to the water may be expected to augment plankton production. The occurrence or non-occurrence of this event is determined by the balance

between (1) the reducing power of the mud, and (2) the amount of oxygen supplied to the mud surface. (2) depends on (a) the volume of the hypolimnion, and (b) the degree of turbulence there. As (a) and (b) are roughly proportional (Fig. 36), it is suggested that, in all but extremely oligotrophic lakes, *morphometric* (including climatic) as well as *edaphic* factors determine the level of productivity.

If, as the result of natural (evolutionary) or cultural changes, (1) is increased sufficiently to effect reduction of the mud surface, productivity may be expected to increase relatively suddenly to a higher level. Examples are quoted.

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## G. E. NICHOLS

## AN APPRECIATION

By NICHOLAS POLUNIN

GEORGE ELWOOD NICHOLS attained eminence in two botanical fields, bryology and ecology. The former was his earlier choice but the latter on the whole his favourite; and whereas in the former he had a considerable reputation in North America, his fame as an ecologist spread much farther afield. Not that his two studies were really separate—rather were they reciprocal or often combined and happily blended. Thus practical experience as an ecologist gave him an acute perception of community and habitat differences that was of great value in his bryological field-work, which, thus developed, itself urged him to give proper recognition to Cryptogamia in his ecological writings; while, more important still, his careful taxonomic and phytogeographical studies of intricate groups of Bryophyta taught him caution in identification and prompted him to check all plant names before publication. Accordingly his ecological papers though not very numerous are authoritative and of lasting value.

Nichols was born at Southington, Connecticut, on 12 April 1882, and died at New Haven in the same State on 20 June 1939. His life was a happy and fruitful one, sadly cut off in its prime; his friendliness was so warm and his personality so vivid that even after two and a half years without him it is difficult to realize that he is not still at work. In all he was a New Englander of the most admirable stamp.

After receiving his early schooling at Southington, Nichols entered Yale University in 1900 and thus began an association which lasted throughout the remainder of his life. He obtained the B.A. degree at the end of the usual four years of residence and then, with the title of Assistant in Botany, he aided in the work of his Department while gradually qualifying for the degree of Ph.D., much prized at Yale; this he was granted in 1909 for a most pains-taking 'Morphological Study of *Juniperus communis* var. *depressa*' (*Beih. Bot. Zbl.*, 1910). Thereupon he was appointed Instructor in Botany, becoming Assistant Professor in 1915, Associate Professor in 1924, and attaining full professorial rank in 1926. This last appointment brought with it the Chairmanship of the Department and the Directorship of the Botanical Gardens, and all three offices he held with distinction and sustained vigour until his death. From 1920 onwards he also served on the staff of the University of Michigan Biological Station at Douglas Lake in the north of the Michigan Peninsula, where he gave attractive summer courses on the taxonomy of the

Algae and the Bryophyta. He was an active member of many scientific societies in the United States, including Sigma Xi; of the Botanical Society of America he was Treasurer in 1925–32 and Vice-President in 1933; of the Ecological Society of America he was President in 1932 as well as for a long time a member of the editorial board; in 1938, in token of the esteem in which he was held also in Bryology, he was elected President of the Sullivant Moss Society. This office he held until his death. He also served for a time on the National Research Council and during the last war as adviser to the American Red Cross on the collection and preparation of Sphagna for surgical dressings.

In bryology, Nichols published some 25 papers; his ecological contributions were of similar number but usually of greater length. In both subjects he taught most actively and successfully for many years. But whereas his writings in both fields were chiefly concerned with North America, many of his ecological concepts and conclusions have found almost world-wide application, although he himself never left the northern half of the New World. It was above all the ecological study of vegetation that held his enthusiastic interest, and the delimitation and subsequent description and classification of plant communities to this end was undoubtedly his forte. His ideas and methods he stated in three detailed papers (in *Plant World*, 1917; *Ecology*, 1923; and *Proc. Internat. Congr. Plant Sci.*, 1929); their application is well illustrated in his 'Vegetation of northern Cape Breton Island' (*Trans. Conn. Acad.*, 1918). Nichols's other most important series of ecological papers were the seven on 'The Vegetation of Connecticut' which appeared in *Torreya* (1913–14) and *Bull. Torrey Bot. Club* (1915–16 and 1920).

It was, however, through his spoken word that Nichols's influence was probably most felt in ecology. His courses at Yale both in the Osborn Botanical Laboratory and in the field were well attended by undergraduate and graduate students alike, and he took an active part in the teaching also of the flourishing and closely adjacent Yale Forestry School. Apart from pupils, and in addition to a seemingly unending stream of more casual visitors, Nichols had numerous correspondents and friends with whom he liberally exchanged views, and who came from or went to almost all parts of the world. He would receive them with evident pleasure and let them go only when their problem had been solved or at least fully discussed and constructively viewed. A prompt and excellent correspondent, his was also a comfortingly familiar, round and robin-like figure that many looked forward to seeing and hailing at meetings, especially of the A.A.A.S. Such a man may not publish very much but of all people certainly does not live in vain!

It still seems true in ecology (and indicative of its youthfulness as a science) that an individual worker's ideas and methods may to a large extent depend on the more striking phenomena obtaining in the region in which he was brought up—at least ecologically speaking. This is perhaps only in continuation of a laudable tendency to be interested in and desire to unravel the

intricacies of one's own *oikos*, but it may be unsatisfactory in leading to limitation of outlook and of angles of approach. Far from subscribing to such faults, Nichols warned others against them, for with his nimble mind he realized early that different methods of attack were needed not only with different problems in the same region but also often with apparently similar problems in different regions. From early visits to Jamaica and to what may be termed the Chicago school of dynamic ecology he brought back clear ideas of the ever-changing nature of vegetation; but though succession was always a theme with him it did not necessarily lead the way; nor for that matter did physiognomy or floristic composition, which are both so complicated and changeable on the recently deglaciated Atlantic seaboard. Rather he attempted to combine all these approaches into an elastic working scheme, in whose application he wisely confined himself to those regions whose physiography and flora he knew most intimately. Many might study his example with advantage, for by such means did he effectively point the way to the ecological elucidation of many of the particularly difficult regions of eastern North America. For this alone ecologists owe him a great debt.

Of Nichols the Professor there is still more to say. Administering his Department always with commendable tact, his keen critical faculties and excellent literary ability were of benefit to many generations of students as well as to his readers and friends. He would spend a whole week-end considering the research problems of a pupil. Just as he would rewrite his own papers again and again, weighing every word until he was certain that *others* would understand exactly what he intended to say, so he would often make a student recast or even begin again if he thought it necessary. In this he rarely if ever proved wrong, and rarely if ever failed to bring forth grateful acknowledgement in the end for what at first often appeared harsh treatment. Even his lectures he always wrote out in full and read aloud, 'so as to be sure not to miss anything, Big Boy'. Always sure also of his facts or else admitting doubt, he would study and describe phenomena as they were and as they affected his world 'rather than worry about their possible mode of origin in the dim and distant past'; in like manner, whenever one tried to persuade him to cross the Atlantic on a visit he would reply that there was still far too much to do at home. His greatest pride in his laboratory was his magnificent and probably unrivalled collection of lantern slides illustrating North American vegetation and ecology, the vast majority of which were the direct outcome of his own skill as a photographer. His *bête noire* was the avalanche of complicated and often obscure terms 'for simple phenomena' which descended upon ecology in his life-time; he would wince and gnash his fine New England teeth if one dared to call a spade a geotome!

As a botanist Nichols will be further remembered by three mosses and one phanerogam named in his honour, viz. *Dicranella Nicholsii* R. S. Williams, *Hygrohypnum Nicholsii* Grout, *Sphagnum Nicholsii* Warnst., and *Salix calc-*

*cola var. Nicholsiana* Polunin. As a man, no colleague or friend or pupil could well forget him. Supremely happy in his family life, and justly proud of his three attractive daughters (his charming wife might almost have been a fourth) and of his replica ‘young George’, he was a free and generous host and, it often seemed, the very best ‘company’ in the world. In the ‘Commons’ on Alumni Day, after the singing of ‘For God, for Country, and for Yale’—the emphasis on such occasions being often on the last—there would be many calls for ‘George’; among his more favoured students he was delightedly referred to as ‘Pop’. Truly his example was one to be studied, and his generous sympathy as a friend and adviser, as well as his energetic personality and infectiously happy smile, were all vital things that cannot be replaced.

## REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

VOL. 10, NO. 2, NOVEMBER 1941

THIS number, of 201 pp., contains seven original papers, five reviews, and 103 Notices of Publications on the Animal Ecology of the British Isles, again witnessing the strong resilience of naturalists and ecologists under the difficult conditions of war-time work. A high proportion of these and of papers that have been since submitted represents research completed before the war or in its early stages; but it is to be expected that the results of ecological investigations done in connexion with the war itself will soon become available to maintain the output of original papers.

James Fisher and George Waterston contribute the results of a very comprehensive enquiry into the present breeding distribution of populations of the fulmar (*Fulmarus glacialis*) in the British Isles, and its extraordinary spread from St Kilda over a wide area since 1878. The report is well illustrated with maps and photographs, and contains the detailed case histories of all colonies that are known about, and a bibliography of 800 references. Dennis Chitty and Helen Chitty present the fifth annual report of the Canadian Arctic Wild Life Enquiry, recording changes of abundance of arctic foxes, snowy owls and lemmings at a number of points from which observers send in reports each year; also sledge dog pandemics. The story for the years 1935 to 1940 is summarized to illustrate the behaviour of the short-period Arctic cycle. There is a good air photograph of the barren lands of Quebec Peninsula.

There are two papers on fresh-water ecology. T. T. Macan and A. MacFayden describe the water bug fauna of dewponds in Wiltshire and Sussex, from a survey of eighty-six dewponds, fifty of which contained water bugs. Twenty-six species were found, the occurrence in different ponds being partly correlated with factors such as permanence and the pollution caused by sheep. K. Radway Allen gives the third instalment of his investigation on the biology of the early stages of the salmon, with reference to populations in the Thurso river system in Caithness. In this paper he concentrates upon the effects of food supply, temperature and other factors on the growth of the young.

There are two papers on marine and estuarine Crustacea. D. M. Reid describes the Amphipod fauna of an almost land-locked sandy lagoon on the coast of Sutherland; while C. B. Goodhart records the estuarine distribution of Amphipoda in the river Afon Water which runs out by the Solent, and also gives a list of species found in the Solent outside. The distribution of various species is correlated with tidal limits and salinities.

A monograph by John Deal, upon the temperature preferendum of certain species of insects, gives details of the apparatus employed for this purpose, and shows that the preferred temperature is usually not a point but has a fairly wide range between definite limits.

Reviews deal with the *Journal of Ecology*; the management of trout streams and their ecology; the present status and past changes in status of wild geese and ducks in the British Isles, and conditions affecting them; animals influencing regeneration of Douglas fir forests in Oregon and Washington; and Fraser Darling's island surveys.

CHARLES ELTON

**V. J. Chapman (1941).** *An Introduction to the Study of Algae.* 387 pp., 209 figs. Cambridge University Press, London. Price 18s.

THIS volume is intended to meet the need of University students reading for a degree course, and is noteworthy for the inclusion of chapters dealing with the ecology and physiology of the algae. The subject-matter, which includes fresh-water and marine algology, comprises a study of the algal groups and their reproduction as well as various aspects of their physiology and ecology. The book has numerous illustrations together with a large number of schematic diagrams illustrating various aspects of the life histories of many of the algae. Some of the illustrations are original but the majority have been taken from other sources. Unfortunately, some of these latter have suffered a little in reproduction.

In dealing with the algal groups, the author has paid most attention to the Chlorophyceae, Xanthophyceae, Cyanophyceae, Phaeophyceae and Rhodophyceae. To the remaining groups a few pages only are devoted and the Diatoms receive very brief treatment, though the chapter is starred as being essential for the study of students in their first and second year. The selection of examples in the main groups includes a large number of types which are extra-British. This doubtless widens the usefulness of the volume, though it may not necessarily constitute the best approach to the subject to a student doing practical work on this side of the Atlantic. Great care has been taken to prepare schemes illustrating life histories and possible inter-relationships between the groups.

References are made to literature where they are considered desirable and the author explains in the Introduction that the choice of such has been a personal matter. From so vast a field it is obvious that rigorous selection had to be made, but even so, there are some surprising omissions, as for example, the work of Sauvageau on the Laminariaceae and Eclipsiophyceae and the researches of Pearsall on the ecology of fresh-water algae.

After concluding the study of the main groups of algae, the author has written a very useful survey of their reproduction and possible evolution, correlating his remarks with the evidence from the fossil record, in so far as that is possible. The chapter which follows deals with Physiology, Symbiosis and Soil Algae, the book concluding with a very helpful section dealing with various aspects of marine and fresh-water ecology. These later chapters present material which has not formerly been available to the student in a collected form and will therefore be of especial value.

It is unfortunate that the volume shows some signs of hurried preparation, as for instance in the inconsistent use of the terms 'group', 'class', 'order' and 'family' in the chapters dealing with the Cyanophyceae and Chlorophyceae. Nevertheless, it will doubtless fill a real need in departmental libraries and will be of great value to students of algology.

L. NEWTON

**PAPERS OF ECOLOGICAL INTEREST  
RECEIVED**

- Blake, S. T.** The vegetation of the Lower Stanley River basin. *Proc. Roy. Soc. Qd.* **42**, 62, 1941.
- Blake, S. T.** The vegetation of Goat Island and Bird Island in Moreton Bay. *Qd Nat.* **9**, 94, 1940.
- Chapman, V. J.** A note on the geological work of mangroves in Jamaica. *Proc. Geol. Ass., Lond.*, **51**, 346, 1940.
- Davies, G. N.** An investigation of the effect of zinc sulphate on plants (comparison with poisoning from lead mines). *Ann. Appl. Biol.* **28**, 81, 1941.
- Fogg, G. E.** Gas vacuoles of the Myxophyceae. *Biol. Rev.* **16**, 205, 1941.
- Forest, H. de & Miller, E.** Some environmental conditions of a Southern California chaparral. *Univ. South California, Gen. Biol. Ser.* No. 1, 1941.
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- Iyengar, M. O. P.** Algal problems peculiar to the tropics, with special reference to India. *Proc. Twenty-fifth Ind. Sci. Congr.* Part 4, 1939.
- Jenkin, B. M., Mortimer, C. H. & Pennington, W.** The study of lake deposits. *Nature, Lond.*, **147**, 496, 1941.
- Ludi, W. & Strussi, B.** Die Klimaverhältnisse des Albisgebietes. *Veroff. Geobot. Inst. Rubel*, **18**, 1941.
- Matthews, J. R.** The ecological approach to land utilisation. *Scot. For. J.* **53**, 22, 1939.
- Moon, H. P. & Green, F. H. W.** Water meadows in Southern England. *Land Utilis. Surv. Rep.* **89** (Hampshire), p. 373, 1940.
- Neilson-Jones, W.** Biological aspects of soil fertility. *J. Agric. Sci.* **31**, 379, 1941.
- Richards, P.** Lowland tropical podzols and their vegetation. *Nature, Lond.*, **148**, 129, 1941.
- Steers, J. A., Chapman, V. J., Colman, J. & Lofthouse, J. A.** Sand cays and mangroves in Jamaica. *Geogr. J.* **96**, 305, 1940.
- Van Raalte, M. H.** On the oxygen supply of rice roots. *Ann. Bot. Gard. Buitenzorg*, **51**, 43, 1941.

## BIOLOGICAL FLORA OF THE BRITISH ISLES

### ACCOUNTS PUBLISHED OR IN PREPARATION

The accounts already published are:

- Juncus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. inflexus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. effusus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. conglomeratus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. subnodulosus* Schrank., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- Zostera* L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
- Z. marina* L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
- Z. Hornemanniana* Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.
- Cladium Mariscus* R. Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1 at 1s. each. Standing orders for all parts issued may be placed at the reduced price of 9d. each.

The following are being prepared:

- Acer Pseudo-platanus* L., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
- Aconitum anglicum* Stapf., H. A. Hyde, National Museum of Wales, Cardiff.
- Adoxa Moschatellina* L., Prof. M. Skene, The University, Bristol.
- Allium ursinum* L., T. G. Tutin, Department of Botany, The University, Manchester.
- Allium vineale* L., Miss R. H. Scott, Botany School, Cambridge.
- Andromeda Polifolia* L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield, 10.
- Asperula odorata* L., Dr A. R. Clapham, Department of Botany, Oxford.
- Aster Tripolium* L., by V. J. Chapman.
- Blackstonia perfoliata* Huds., Dr B. Colson, Department of Botany, Reading.
- Corallorrhiza trifida* Chatel. emend., Prof. J. R. Matthews and Dr Downie, Department of Botany, Old Aberdeen.
- Eriocaulon septangulare* With., Dr Leighton Hare, Jodrell Laboratory, Kew Gardens, Surrey.
- Frangula Alnus* Mill., Dr H. Godwin, Botany School, Cambridge.
- Galium erectum* Huds. and *G. Mollugo* L., Miss M. Priestley, Botany School, Cambridge.
- Glyceria maxima* (Hartm.) Holmb., Miss J. M. Lambert, Department of Botany, The University, Sheffield, 10.

- Goodyera repens* R. Br., Prof. J. R. Matthews and Dr Downie, Department of Botany, Old Aberdeen.
- Juncus articulatus* L. and *J. acutiflorus* Hoffm. (*J. sylvaticus* Reich.), Dr A. R. Clapham, Department of Botany, Oxford.
- Juncus macr* Gray and *J. filiformis* L., Dr P. W. Richards, Botany School, Cambridge.
- Juncus squarrosum* L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield, 10.
- Juniperus communis* L., T. G. Tutin, Department of Botany, Manchester.
- Leucojum aestivum* L., Dr F. B. Hora, Department of Botany, Reading.
- Limosella aquatica* L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower Street, London, W.C. 1.
- Listera cordata* R. Br., Prof. J. R. Matthews and Dr Downie, Department of Botany, Old Aberdeen.
- Luzula pilosa* Willd. and *L. Forsteri* DC., Prof. T. Harris, Department of Botany, Reading.
- Melandrium dioicum* (Mill.) Garcke and *M. album* (Lemend.) Simonk. (*Lychnis*), H. G. Baker, Hosa Research Laboratories, Windmill Road, Sunbury-on-Thames, Middlesex.
- Myosotis arvensis* (L.) Hill, *M. versicolor* Sm. and *M. collina* Hoffm., A. E. Wade, National Museum of Wales, Cardiff.
- Narthecium ossifragum* Huds., Dr Mollison, Department of Botany, Old Aberdeen.
- Rhamnus catharticus* L., Dr H. Godwin, Botany School, Cambridge.
- Rhynchospora alba* Vahl. and *R. fusca* Ait. f., Miss E. Canton, Department of Biology, The Technical College, Sunderland.
- Scilla non-scripta* (L.) Hoffm. & Link., G. E. Blackman, Imperial College of Science, London, S.W. 7.
- Sonchus asper* Hoffm. and *S. oleraceus* L., R. A. Lewin, Botany School, Cambridge.
- Tamus communis* L., I. H. Burkill, F.L.S., Clova, The Mount, Leatherhead, Surrey.
- Tilia cordata* Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.
- Trientalis europaea* L., Prof. J. R. Matthews, Department of Botany, Old Aberdeen.
- Valeriana officinalis* L. and *V. sambucifolia* Mikan., J. Carpenter, Botany School, Cambridge.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account, singly or in collaboration, should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

*CLADIUM P.Br.*

One British species

**Cladium Mariscus** (L.) R.Br. (*C. germanicum* Schrad.; *C. jamaicense* auct. non Crantz; *Mariscus serratus* Gilib.)

V. M. CONWAY

A coarse perennial sedge, strongly gregarious, 80–200 cm., with upright rootstocks and horizontal rhizomes. Leaves evergreen, glaucous, very hard, tapering to a narrow, three-sided, usually withered tip, up to  $300 \times 1.0\text{--}1.5$  cm.,

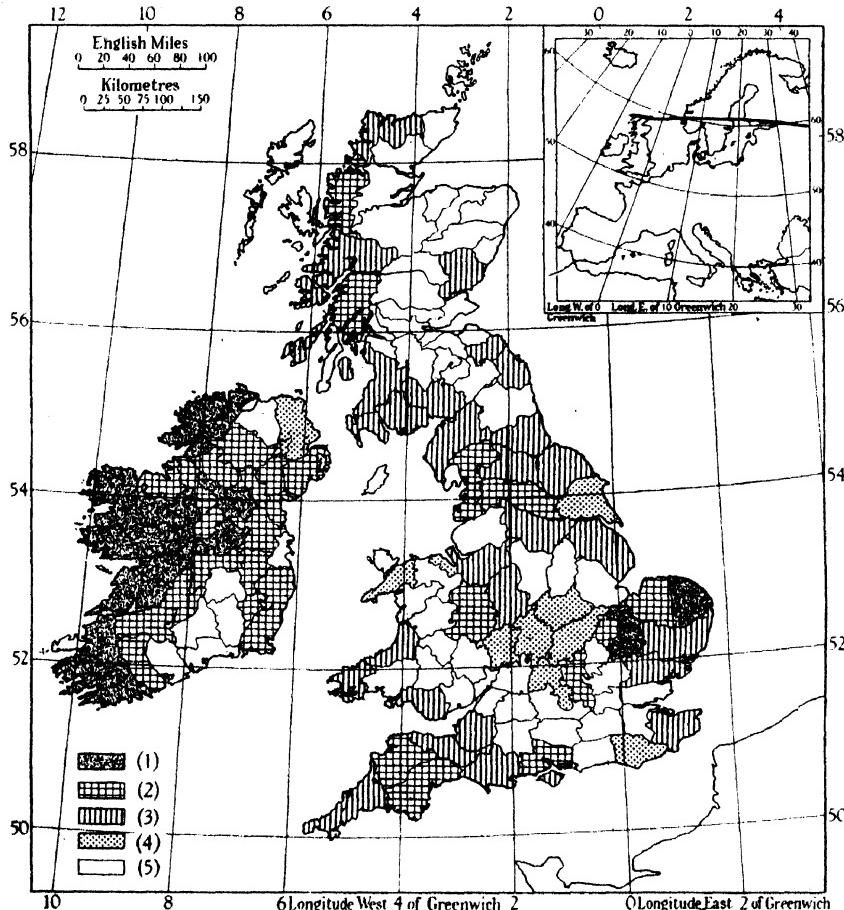


Fig. 1. *Cladium Mariscus* R. Br.: vice-comital distribution in the British Isles and (inset) northern limit in Europe. (1) Occasional to abundant. (2) Rare (from one to six localities). Records later than 1918, or confirmed by unpublished observations. (3) Rare. Data found by the writer only in Druce (1932) or in floras published before 1918. (4) Known to have become extinct during the last 120 years, or given as doubtful by Druce (1932). (5) Absent.

the keel and margins in the distal part bearing short hard spines that give sharply cutting edges. Flowering stems terete, 100–200 cm. Spikelets rusty

brown, terete, 3–4 mm., in small very numerous clusters, arranged in one terminal and several lateral cymes, the whole inflorescence forming a more or less leafy oblong panicle. Flowers two to three in the spikelet, the terminal ♂, the lower ♀, with a number of empty glumes below. Bristles 0. Stamens usually 2. Nut brown, ovoid, trigonous, beaked, its outer covering thick and fleshy.

A species of temperate to subtropical climates, helophytic, basicolous and intolerant of shade.

I. *Distribution.* Scattered throughout the greater part of England, Wales and Scotland, locally abundant in East Anglia, elsewhere very scanty and becoming increasingly rare. Throughout most of Ireland, but much more abundant in the west than in the east.

Throughout Europe south of lat. 60°, though scarce east of long. 25° E., where it occurs south of a line from Lakes Ladoga and Ilmen and the Upper Volga south-eastwards to Turkestan, Pamir, and Kashmir; Mediterranean, including Tunis, Asia Minor; Crimea, Caucasus, Transcaucasia, Iran. The South African species is doubtfully the same. Closely related species are found in North and South America and the West Indies (*C. jamaicense* Crantz, etc.); in East Asia, Hawaii, and Australia.

A lowland species in Britain; to 830 m. in Tyrol, when, however, it is usually sterile (Hegi), 850 m. in Graubünden (Braun-Blanquet & Rübel, 1932).

II. *Habitat.* (1) Shallow-water zones in lakes and ponds and the fens that may adjoin these or develop from them.

(2) *Substratum.* Peat, or mineral soils rich in organic matter, and in Connemara, near the coast, in small lakes with a floor of marine sand (Pearsall). In the Norfolk Broads region extensive floating mats may be formed over the water surface.

(c) *Water table.* It is essential that the water table should usually be above the root level, i.e. not more than about 15 cm. below soil level, though short periods of lower level in summer can be tolerated. A depth of more than 40 cm. of water above the soil level is unfavourable, possibly operating through water-logging of the decayed dead leaf-bases (Conway, 1937). Between these limits the soil level/water level relation seems a matter of indifference except in so far as it may decide whether or not the growing-point is subjected to frost (von Post, 1925). See V(c). When it occurs in oligotrophic bog-communities it indicates the position of former open water (Praeger, 1934).

(g) *pH.* It seems in general that a *pH* of 6·0 or over is required. Values at Wicken Fen (Godwin *et al.* 1932) showed 7·5 as the mean of forty-eight estimations, extreme values 6·5 and 8·5 (colorimetric, depths from 5 to 15 cm.). The water of the Norfolk Broads is also alkaline (Godwin). When *C. Mariscus* is associated with acidicolous species such as *Sphagnum squarrosum* the root-systems appear in peat of *pH* 6·1–6·4, but the surface may be as acid as *pH* 4·3 (Godwin & Turner, 1933). The majority of Irish localities occur in limestone regions. Apparent exceptions occur in Connemara (Praeger,

1934) where the species, together with other calcicoles, seems to be flourishing in acid bog conditions. In cases of this type examined by Pearsall, *Cladium* was rooted in coarse base-saturated sands with a pH in two examples of 6.13 and 6.44 (electrometric), or else in marine sand.

(h) *Humus content* (Bharucha, 1932). Mean of fourteen estimations in Wicken Fen peat at varying depths up to 80 cm., 74%.

(i) *CaCO<sub>3</sub> content* (Bharucha, 1932). Five samples from the upper 20 cm. at Wicken showed mean value 0.25% dry weight. (Deeper samples were richer owing to the local influence of a chalk marl layer.)

Data under (h) and (i) are probably representative for all the East Anglian localities.

(3) (a) *Light intensity*. Will not tolerate shade, and dies out after invasion by bushes, though it does so very gradually, and living shoots may be present beneath bushes of 20 years or more in age (Godwin, 1936).

.. (b) *Air humidity*. Provided that the roots are growing in water, the growth of the plant is strongly correlated with bright sunshine and high temperature, and hence, roughly speaking, with the dryness of the atmosphere.

(c) *Wind exposure* causes the withering of the distal ends of the leaves, especially in late autumn, but this does not appear to damage the general vigour of the plant if other factors are favourable.

III. *Communities*. Characteristic of (a) reed-swamps in shallow water, following *Phragmites* in the hydrosere; (b) the fens developing from (a) by the rise of soil level by peat accumulation ('Verlandung' stage). It remains as a fen component until quite overshadowed by the bushes of the normally succeeding swamp woodland. It may grow so densely as to exclude all other species, this dominance operating largely through its evergreen habit and the long persistence of the dead leaves as a thick 'leaf-mattress' (Godwin & Tansley, 1929). Where less dense, its most constant associates are (1) in reed-swamps, *Phragmites communis*; (2) in the fen communities in East Anglia, *Carex stricta*, *Juncus subnodulosus*, *Hydrocotyle vulgaris*, *Galium palustre*, *Myrica Gale*, *Lythrum Salicaria*, *Eupatorium cannabinum*; (3) in the latest stages of fen, seedlings and young bushes of *Salix atrocinerea*, *Alnus glutinosa*, *Frangula Alnus*; (4) in places where the fen vegetation is cut at intervals, e.g. Wicken 'Mixed Sedge', Norfolk Broads 'mowing meadows', *Molinia coerulea*, *Schoenus nigricans*, *Carex panicea*, *Juncus subnodulosus*, *Salix repens* var. *fusca*, *Hypnum cuspidatum* and many other fen species. It is sometimes associated with base tolerant *Sphagna*, such as *S. squarrosum*, and *Eriophorum angustifolium* (Godwin).

IV. *Response to biotic factors*. Owing to their toughness and durability the leaves have long been used in East Anglia for thatch by themselves or as a capping to *Phragmites* thatch: regular cropping for this purpose is still carried on locally. The plant can withstand being cut to ground level if this does not take place more often than once in 4 years. With more frequent cutting it becomes more and more reduced in vigour and finally dies out. It is never

grazed. Burning and trampling have parallel effects to those of cutting: the 'dead-leaf mattress' is very readily inflammable and the dried leaves of *Cladium* were formerly used as kindling.

V. (a) *Gregariousness*. Highly gregarious, owing to the nature of the vegetative reproduction.

(b) *Performance in various habitats*. Height variable, leaves up to 300 cm. long but bending over at a uniform height of 100–200 cm., and inflorescences 150–200 cm. in dense stands in typical sedge vegetation. The height may be greater in the shade of invading bushes. When persisting under unfavourable conditions of cutting or drought, the shoots are dwarf and the leaves narrow. The species flowers best when growing in sunny open positions in completely submerged soils. Flowering frequency varies greatly from one summer to another. Over the great part of its British range flowering is infrequent (Godwin).

(c) *Effect of frost, drought, etc.* Underground regions of the plant are frost sensitive, the rest is not, unless the air temperature falls below  $-10^{\circ}$  C. (Conway, 1938).

VI. (a) to (g) *Morphology, etc.* The evergreen foliage leaves of a particular shoot are produced from an upright rootstock which has its base about 20 cm. below soil level (under Wicken Fen conditions). Rhizomes grow out horizontally from the upright rootstock, most commonly when the latter is in its second or third year of growth. The rhizomes grow obliquely downwards if exposed to light (Raunkiaer, 1934). The apex of the rhizome turns upwards and develops into a new shoot. The growing point remains underground until it develops into the flowering stem. This does not happen until the shoot has produced five to seven full-sized foliage leaves, and von Post (1925) quotes a statement by Raunkiaer that 3–4 years are needed before the shoot will flower. In all habitat conditions at Wicken, the maximum height of rootstock appears to be about 12 cm., which indicates a maximum life of each shoot of 7 years (calculating from means of observations on number of leaves produced per annum and number of leaves per cm. of stock). The distance between a shoot and its parent shoot varies with conditions, being greater when growth is vigorous. The maximum yet found is 25 cm., the most usual distance being 15 cm. The latter would give as the maximum rate of vegetative advance of a clone something of the order of 1 m. in 12 years. Roots are produced from the upright stock, not from the horizontal rhizomes which bear only scale leaves. When growing in water the roots are thick, waxy, sparingly branched, directed horizontally or obliquely downwards. In moist but not submerged soils they are fibrous and form a dense mat. Mycorrhiza has never been observed.

(h) *Frequency of seed production*. Seed is set in every inflorescence, but see sections V (b) and VII (e).

(i) *Ecotypes*. No ecotypes are known.

(j) *Chromosome number*. Chromosome number has not been investigated. Mitotic nuclei in the leaf meristem are exceedingly small.

VII. *Phenology.* (a) Time of maximum growth of roots not known directly, but likely to coincide with that of the leaves.

(b) The frequency of appearance of new leafy shoots is parallel to the growth of the leaves on the older shoots, i.e. a maximum in the summer and zero in the winter months.

(c) Time of flowering June to mid-July in East Anglia. No data for other districts.

(d) Seeds matured and shed from September to December.

(e) Seedlings have not yet been found by the writer, and all attempts to make seeds germinate have failed.

VIII. (a) *Mode of pollination.* Pollination by wind.

(c) *Cleistogamy.* Not reported.

(d) *Apomixis.* No information.

(e) *Vivipary.* Never observed.

(g) *Amount of seed.* Fruits one-seeded; probably from 500 to 1500 fruits per inflorescence, according to degree of luxuriance.

(h) *Dispersal.* Ridley (1930) states '...the oval nuts float (according to Praeger, 1913) for 15 months or more. It probably owes its actual wide distribution to the attachment of its nuts to the feet of wading birds, but in places where it is very abundant, as in the Norfolk Broads, its local distribution is no doubt due to its floating nuts. Ravn (1894) states that its nuts have dry flesh composed of air-cells with thin walls and large intercellular spaces. The seeds sink readily if the flesh is removed.'

(l) *Effective reproduction.* Although vegetative reproduction appears to be entirely predominant in East Anglia, there is evidence of recent colonization by seed in Sweden (von Post, 1925), and further information on this subject is much needed for British localities.

IX. *Parasites : diseases.* No insects are especially associated with *Cladium Mariscus* and very few are recorded to feed on it at all (O. W. Richards).

The following fungi have been reported, but there is no evidence that serious diseases are caused by any of them.

#### BASIDIOMYCETES

**HYMENOMYCETES:** *Puccinia Cladii* Ell. and Tr., *Peniophora cinerea* (Fr.) Cooke, *Marasmius Menieri* Bond., *Omphalia gibba* Pat., *Pistillaria aculeata* Pat.

#### ASCOMYCETES

**DISCOMYCETES:** *Helotium eburneum* (Desm.) Gill, *Phragmonaevia hysterioides* (Desm.) Rehm.

**PYRENOMYCETES:** *Metaspheeria cumana* (Sacc. & Spieg.) Sacc., *Niesslia exosporioides* (Desm.) Wint., *Ophiobolus helicosporus* (Berk. & Br.) Sacc.

#### FUNGI IMPERFECTI

**COELOMYCETES:** *Pestalotia caudata* (Syd.), *Leptostroma caricinum* Fr., *Stagonospora Caricis* (Oud.) Sacc.

HYPHOMYCETES: *Tetraploa aristata* Berk. & Br., *Torula rhizophila* Corda,  
*Volutella arundinis* Desm.

The above list has been compiled chiefly from the following sources:

- CORNER, E. J. H. (1935). The Fungi of Wicken Fen, Cambridgeshire. *Trans. Brit. Mycol. Soc.* **29**, 280-87.  
ELLIS, E. A. (1940). The Natural History of Wheatfen Broad, Surlingham. Pt. III. *Trans. Norf. Norw. Nat. Soc.* **15**, 191-219.

X. *History.* The subfossil fruits are easily recognizable, as are also the rhizome fragments which have a black cortex containing a parallel bundle system inside a bright brick-red matrix. *Cladium* peat is abundant and often thick, occurring frequently as a late stage in the infilling of lakes or lagoons above *Phragmites* peat and below wood or *Sphagnum* peat (Godwin). The species has been recorded throughout post-glacial times as far back as the Boreal, and possibly in the Pre-Boreal (Clapham, A. R. & B. N., 1939). The records are not confined to the present areas of relative abundance but are derived also from regions such as Tregaron, Cardiganshire (Godwin & Mitchell, 1938), where the species is not now found. In Sweden the fossil records are sufficiently numerous to allow the conclusion (von Post, 1925) that the species was much more widespread and abundant in Boreal and early Atlantic times than at a later period, though in recent times there has been renewed spread. von Post also suggests that the scanty distribution of the species at the present day is not due to unsuitable climatic conditions but to human activity in draining lakes and fens. The same probably holds good for Britain.

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**ZOSTERA L.**

T. G. TUTIN

There are three British species, in the following two sections:

**ALEGA.** Flowering stems branched, seeds longitudinally costate, *retinaculae* absent or only rarely occurring at the bottom of the spadix, leaf sheaths closed and bundles of strengthening tissue in the outermost layers of the cortex of the stem. *Zostera marina*, *Z. Hornemanniana*.

**ZOSTERELLA.** Flowering stems unbranched, seeds smooth, *retinaculae* always present, leaf sheaths open, and strengthening tissue only in the inner layers of the cortex of the stem. *Z. nana*.

These species are not known to hybridize.

**Habit.** All the species are submerged perennial herbs with a creeping rhizome and erect flowering stems. Each rhizome segment terminates in an inflorescence, growth being continued by lateral branches which become separated by the death of the parent rhizome.

**Leaves.** The leaves are long, narrow and very flexible, with large intercellular spaces.

**Flowers.** The flowers are unisexual, have no perianth, and are water-pollinated and protogynous. The pollen is thread-like. No species is known to be apomictic. The seeds which are heavier than water are 2-3.5 mm. long and are distributed by water movements and possibly also on the feet of wading birds.

**Seedlings.** Observations have only been made on the two species in section Alega. The seeds have been observed to germinate in autumn and winter. The plumule emerges from the testa and is carried upwards by the elongation of the hypocotyl. The primary root does not develop, and adventitious roots arise at each node of the rhizome.

**Life-form.** All the species are hydrophytes.

**Ecology.** All the species grow submerged in salt or brackish water where they are exposed only for short periods at low tide, if at all.

L.C. No. 1979 (11th edition).

**ZOSTERA MARINA L.**

**Sect. ALEGA.** Leaves 0.5-1 cm. broad, stigma twice as long as style, seeds 3.5 mm. long. Varies considerably in size and luxuriance. Leaves on flowering stems, and foliaceous continuations of the spathe, much narrower than leaves of sterile shoots.

Marine, rarely found in estuaries or brackish water.

**I. Geographical and altitudinal distribution.** Local but fairly well distributed along the south coast and the coast of East Anglia, becoming rarer north-

wards. Apparently less common in Wales and north-west England. Recorded from most of the Irish coast. Records unsupported by specimens must be regarded with doubt, as *Z. Hornemanniana* is frequently confused with this species. Circumboreal. In Europe from the Mediterranean to Norwegian Lapland (lat. 71° N.), west Greenland (64° N.), Atlantic and Pacific coasts

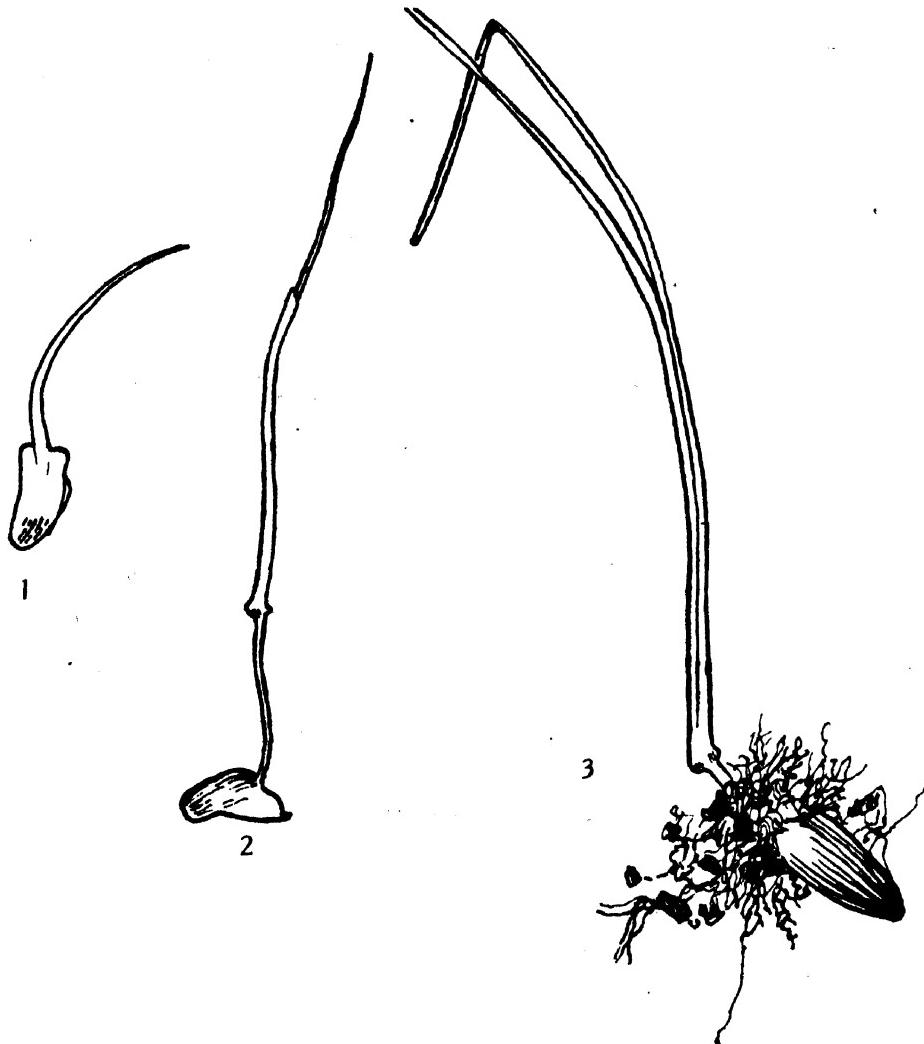


Fig. 1.

of North America from N. Carolina to Hudson's Bay, and California to Unalaska Bay (Setchell, 1929). No maps are included with these accounts as the distribution is not known sufficiently to justify them. It is probable that both species occur in all suitable habitats in the British Isles.

It occurs from slightly above, to 4 m. below, L.W.O.S.T. in the British Isles, but extends down to 10 m. in the Mediterranean (Fiori & Paoletti, 1896-8). It is restricted to regions of moderate shelter as excessive wave

action uproots it, and is generally absent from places where the salinity falls much below 35 g./l.

II. *Habitat.* Bays, sea lochs, and estuaries with little land drainage coming into them, more rarely salt-marsh creeks; in shallow water sheltered from waves. Substratum very variable, ranging from soft mud to gravel mixed with coarse sand. Most often found, in the British Isles, on firm muddy sand, often covered with a coarser layer. No chemical analyses of the substratum have been made, but presumably the soil water is more or less in equilibrium with the sea water above it. It is possible that absorption goes on over the leaf surface, and the plant may therefore in any case be more or less independent of the chemical nature of the substratum.

The light intensity on *Zostera* beds is correlated with the degree of wave action, type of bottom, and depth of water, and is certainly very variable. No actual measurements are available, but Kitching *et al.* (1934) state that after a storm in a locality with a sandy bottom, visibility was reduced to about 2 ft., while in a Scottish loch with a mud bottom under similar circumstances work in a diving helmet in shallow water was impossible owing to turbidity. Diatoms, other small algae, and hydroids, which are epiphytic on all but the youngest leaves, and more particularly the silt held by these epiphytes, must materially reduce the light reaching the photosynthetic surface. Even in calm conditions the absorption coefficient of light in inshore waters is very variable (Cooper & Milne, 1938). There can be little doubt that light is generally, if not always, limiting to the growth of the plant in deep water. The upper limit of growth is fixed by the degree of drying to which the plant is subjected at low tide. This depends on the type of bottom and the local characteristics of the tidal cycle. The upper layers of a sandy substratum dry out rapidly when exposed, while mud remains moist and holds numerous shallow pools of water. In sandy localities the plant grows in stations where it is exposed only at L.W.O.S.T., while on mud it may grow so much higher above L.W.O.S.T. that it will be exposed at most tides. The time of low water full and change is also of importance, as this affects the amount of drying during the period of exposure. It is probably for this reason that the plant grows at higher levels on the west coast of Scotland, where L.W.O.S.T. is about 6 a.m. and 6 p.m., than in south Devon where it is about noon and midnight. The double tides in the neighbourhood of the Isle of Wight are probably responsible for the unusually high level at which the plant occurs there, as the period of exposure is shorter than it would normally be.

III. *Communities.* Usually pure, apart from epiphytic algae. In the Fleet, Dorset, mixed with *Ruppia*. According to Flahault (1908) common associates in the western Mediterranean are *Enteromorpha compressa*, *E. ramulosa*, *Codium tomentosum*, *Sphacelaria scoparia*, *Padina pavonia*, *Dictyota dichotoma*, *Gracilaria confervoides*, *Gelidium latifolium*, *Ceramium rubrum* and, in summer, *Acetabularia mediterranea*. The following animals are evidently associated with

*Zostera marina* on the coast of south Devon, since they have either disappeared or become very rare since the pronounced decrease in the amount of *Zostera* in 1932-4.

Gasteropoda: *Cantharidus striatus*, *Rissoa membranacea*.

Coelenterata: *Eleutheria dichotoma*, *Haliclystus dichotoma*.

Crustacea: *Hippolyte prideauxiana*.

Fish: *Spinachia vulgaris* (Stickleback), *Entelurus aequoreus*, *Syngnathus acus*, *S. typhila* (Pipe fishes), *Labrus bergylta*, *Crenilabrus melops*, *Ctenolabrus rupestris*, *Centrolabrus exoletus* (Wrasse; young stages).

(Dr M. V. Lebour (in litt.).)

IV. *Response to biotic factors.* In some countries the leaves were collected and used for heat, and particularly sound, insulation. It is estimated that for Denmark the *Zostera* crop exceeded the total hay crop. It is unlikely that this gathering of the leaves in late summer had any detrimental effect on the plant. In North America, *Z. marina* was an important food of various species of geese, which were in turn eaten by Eskimos. The recent serious decrease in the abundance of the plant has had striking repercussions on these animals. There seems to be no evidence that *Zostera* is an important food for sea-birds in this country.

V. (a) *Gregariousness.* Grows in communities varying from 1 to 2 ft. across to great beds the size of which can be measured in acres.

(b) *Performance in various habitats.* In sheltered places with sandy mud the plant attains a height of about 50 cm. and flowers freely; on harder bottoms in greater exposure leaves 10-30 cm. long are produced and the plant rarely flowers. Leaves up to 1 m. long are recorded (Graebner, 1907).

(c) *Effect of frost, drought, etc.* Very susceptible to drought. The shoots are rigid at the base and when exposed stand erect for about 1 cm. and then bend over so that the leaves lie flat on the substratum when exposed. Half an hour's exposure to air on a sunny day may be sufficient to kill the base of the shoot, the leaves remaining green and unharmed temporarily as they are kept moist by contact with the substratum. A very short exposure to air on a sunny or windy day is sufficient to kill the flowers, the stigmas being particularly susceptible. Rain during periods of exposure seems to be without effect on the plant. The plant gets frozen only in very exceptional circumstances; it is said to suffer then from the mechanical action of the ice in tearing off leaves and sometimes uprooting the rhizome.

VI. (a), (b) *Morphology.* Rhizome 2-5 mm. thick with short internodes, creeping and branching freely; in the mature plant each section produces leaves and terminal bud one year, and a flowering stem and leafy branches in the next. The section of rhizome which has borne the inflorescence dies, the dead rhizome persisting for a considerable time. The branches behave in the same way as the parent rhizome. Bunches of adventitious roots (c. 5 cm. long) are produced at the nodes and anchor the rhizome, which most frequently

ies on or very near to the surface of the substratum. It survives being buried to a depth of several centimetres by material swept on to it in storms.

(c) *Mycorrhiza*. None reported.

(d) *Perennation*. Short leaves are produced in autumn and survive the winter. In spring they do not elongate, but die off as the long summer leaves develop.

(e) *Vegetative reproduction*. Short lengths of rhizome break off and are carried by water movements and if deposited in suitable habitats form new colonies. The rhizome generally seems to grow between one and two centimetres a year.

(f) *Longevity*. The plant is perennial and apparently lives for many years. Each rhizome branch behaves as a biennial, while the rootless, erect flowering stems survive only one season.

(g) *Age at 1st flowering*. The plant flowers first in its third or fourth season in var. *typica*, but in the second season in var. *latifolia* growing in Pacific North America (Setchell, 1929).

(h) *Frequency of seed production*. The amount of seed set varies very much from year to year, depending on the continuance of sea temperatures over 15° C., and it is probable that in some years little or no seed ripens.

(i) *Ecotypes*. None known definitely. The variety *latifolia*, known from the Pacific coast of North America, differs from the type in having leaves up to 12 mm. wide, but seems to behave in the same way as the type. It has been suggested that this may be an ecotype (Setchell, 1927). The variety *angustifolia* consists in part of narrow-leaved forms living in unfavourable habitats, but, as far as is known, not differing genetically from var. *typica*. *Z. Hornemanniana* (q.v.) has been confused with this variety.

(j) *Chromosome number*.  $2n=12$  (Blackburn, 1934).

VII. *Phenology*. The temperature relations of the plant were determined by Setchell (1929) by an extensive series of observations in United States waters. They have been confirmed by observation in the neighbourhood of Plymouth, where they were extended to *Z. Hornemanniana* (Tutin, 1938).

(a) *Roots*. No information.

(b) *Shoots*. The plant has leafy shoots throughout the year. These begin active growth, and fresh branches appear at the end of April or beginning of May in South England, when the sea temperature reaches 10° C.

(c) *Flowers*. Flowering begins when the sea temperature reaches 15° C., which is usually in July in South England.

(d) *Fruits*. Seeds mature and are shed mainly in August and September but may be found as late as October.

(e) *Germination*. Seedlings are always scarce and in many years none can be found. Germination appears to occur in the autumn and early winter, in the neighbourhood of parent plants, usually in shallow depressions which remain wet at low tide.

VIII. (a) *Pollination.* Water-pollinated, protogynous. The method is very effective as ripe stigmas are nearly always found to be pollinated. The filamentous pollen remains in suspension for days and is carried about by the convection currents which occur in a tank of still water standing in a room. The pollination is well described by Clavaud (1878).

(c) *Cleistogamy.* Does not occur.

(d) *Apomixis.* Reproduction, as far as is known, is amphimictic.

(e) *Vivipary.* Not observed.

(f) *Hybrids.* The species is not known to hybridize. Cytological examination of putative hybrids between *Z. marina* and *Z. nana* has been made, but no sign of hybridity was shown by these plants (Tutin, 1938).

(g) *Amount of seed.* Each fruit contains a single seed. The number of seeds per spadix varies from five to about eleven, averaging about seven. The average number of seeds per flowering shoot is about sixty.

(h) *Dispersal and special features.* The seeds on each spadix ripen in no definite order and the ripening often extends over a week or more. The seed is enclosed in the green membranous ovary wall which becomes weakened as it matures. It finally splits as result of the slight pressure of the bubble of gas produced inside it by photosynthesis. Fruits kept in the dark fail to dehisce and the seeds rot in situ. The seeds are dispersed by water movements but seldom seem to be carried far from the parent plant. According to Piccone (1885), they are also dispersed by fish. They are killed by short periods of drying and could therefore not be carried far in a viable state on the feet of wading birds, unless perhaps encased in mud.

(i) *Viability.* The viability of the seeds was determined by keeping groups of fifty on filter paper in glass finger-bowls in filtered sea water which was changed at frequent intervals. The bowls were covered with glass plates to reduce evaporation. They were kept under the sets of conditions shown in the following table which gives the number of germinants in certain months (Tutin, 1938).

	Daylight 9-13° C.	Daylight 16° C.	Dark 12-15° C.	Dark 14-16° C.
November	0	0	0	1
January	0	2	3	1
February	6	0	1	7
March	4	0	1	5
April	0	0	2	0
% germinated	20	4	14	28

From this it is difficult to draw any definite conclusion about special conditions affecting germination, though it is evident that the percentage germination is always low; this is confirmed by the rarity of seedlings in the field.

(j) *Conditions for germination.* See preceding paragraph.

(k) *Morphology of seedlings.* When the seed germinates the testa splits longitudinally and the hypocotyl elongates carrying the plumule out. At the

same time the scutellum-like enlargement of the lower part of the hypocotyl develops numerous long hairs. The primary root does not develop, but two adventitious roots are produced from the first node. These grow 2–4 cm. long and several leaves are produced. Then more adventitious roots develop from the same node (Fig. 1). It is not until the second year that the rhizome begins to elongate. A good series of drawings of seedlings of var. *latifolia* is given by Setchell (1929).

(l) *Relative importance of reproduction vegetatively and by seed.* In the British Isles reproduction by vegetative means seems always to be far more important than reproduction by seed.

IX. *Parasites: disease.* A serious disease began to affect the plant in Western European and Eastern United States waters in 1931, and had become general by 1933–4, when it was estimated that 90% of the plants had been destroyed in these regions. Small brown spots develop on the leaves, and these spread and become darker, covering large portions of the leaves, which eventually become detached from the plant. Rhizomes also show discolouration, though not as early, or as distinctly, as the leaves. They frequently survive for a year or more, after the disease becomes evident, but are weakened and eventually killed by the repeated defoliation of the plant. The following have been described as causal organisms: a bacterium (unidentified—Fischer-Piette *et al.* 1932). *Labyrinthula* sp. (Protozoa) (Renn, 1934, 1935, 1936a, 1936b). *Ophiobolus halimus* (Ascomycetes) (Mounce & Diehl, 1934). The two latter have been found to occur frequently in this country. The disease has not been reported from the Mediterranean on var. *typica* nor from the Pacific on var. *latifolia*. There seems to have been little change in the abundance of the plant since 1934, and it may still be found in small quantity in most of its old localities. A vivid description of the effect of the disease is given by Wohlenberg (1935).

X. *History.* No information.

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### ZOSTERA HORNEMANNIANA TUTIN

Sect. ALEGA. Leaves about 0·2 cm. broad, stigma as long as style, seeds 2·5 mm. long. Leaves often only 0·1 cm. wide in winter, when mature notched at the apex.

Generally in estuaries, rarely in the sea.

I. *Geographical and altitudinal distribution.* In the British Isles, apparently similar to that of *Zostera marina*, with which it was confused till recently. So far, only recorded from Denmark and Sweden outside the British Isles (Tutin, 1937). From half-tide mark to low-tide mark, and rarely down to 4 m.

II. *Habitat.* On mud flats and estuaries in water of variable salinity, often about 25 g./l., rarely on sandy substrata, always well sheltered from violent waves. Conditions controlling illumination and the upper limit of growth essentially the same as for *Z. marina*. The present species generally grows in shallower but more turbid water.

III. *Communities.* Usually pure, sometimes associated with *Chaetomorpha* sp., only rarely found in proximity to the other species. *Hydrobia ulvae* (Mollusca) and *Idotea viridis* (Crustacea-Isopoda) are very generally associated with it.

IV. *Response to biotic factors.* Nothing known.

V. (a) *Gregariousness.* Grows in communities of varying size but apparently never so extensive as *Zostera marina*. At high levels the patches are small and limited to slight depressions in the mud.

(b) *Performance in various habitats.* It appears to grow best on soft mud, in depressions where it is always wet at low tide and not deeply submerged at high tide. Grows very feebly and rarely flowers on hard or sandy substrata.

(c) *Effect of frost, drought, etc.* Very susceptible to drought, but more tolerant than *Z. marina*. The mud on which it usually grows remains damp, even at low tide, and since the shoots are flexible enough to lie flat on the

mud surface when exposed, they rarely dry out and frequently remain covered with water in pools 0·5 cm. deep or less. *Z. marina* transplanted to such a habitat was invariably killed (Tutin, 1938). For effect of rain and freezing, see *Z. marina*.

VI. (a), (b) *Morphology*. See *Z. marina*. The rhizome is 1–2 mm. thick and the whole plant smaller and more slender.

(c) *Mycorrhiza*. None reported.

(d) *Perennation*. See *Z. marina*.

(e) *Vegetative reproduction*. See *Z. marina*.

(f) *Longevity*. See *Z. marina*.

(g) *Age at first flowering*. Probably three or four years, but no definite information.



Fig. 2.

(h) *Frequency of seed production*. A considerable amount of seed seems to be set every year in favourable localities, as the flowering season often extends from June to November (Trevol, R. Tamar). This is because the water held in the shallow depressions in the mud at low tide gets warmed to temperatures well above 15° C. (see *Z. marina*) in the summer whenever there is sunshine. The period of exposure in 24 hr. is very long, owing to the high level at which the plants grow, so that for a considerable part of every sunny day the temperature of the water surrounding the plants is suitable for flowering.

(i) *Ecotypes*. None known.

(j) *Chromosome number*.  $2n=12$  (Tutin, 1936).

VII. *Phenology*. (a) *Roots*. No information.

(b) *Shoots*. The temperature relations seem to be much the same as for

*Z. marina* but owing to the special conditions described above (VI (h)) growth may begin early in April and continue till November.

(c) *Flowering*. June to November in the neighbourhood of Plymouth. The later flowers are killed by cold. Production of inflorescences in small numbers continues right up till the end of the growing season.

(d) *Seeds*. Mature and are shed from July to November.

(e) *Germination*. Seedlings occur regularly in small numbers. Germination occurs from November to April.

VIII. (a) *Pollination*. See *Z. marina*.

(c) *Cleistogamy*. Never observed.

(d) *Apomixis*. Reproduction, as far as is known, is amphimictic.

(e) *Vivipary*. Not observed.

(f) *Hybrids*. None known.

(g) *Amount of seed*. Each fruit contains a single seed. The number of seeds per spadix averages four, and varies between two and seven. The average number of seeds per flowering stem is about seventy. Owing to the longer flowering season the annual seed production of the plant is undoubtedly greater than in *Z. marina*.

(h) *Dispersal and special features*. See *Z. marina*. Counts of the number of seeds per sq. m. between 0 and 50 cm. and 50 and 100 cm. from the plant were made between November and February at Trevol, R. Tamar and gave an average of 70 and 11 respectively. In the first group an average of 55 seeds were dead, while in the second, only one living seed was found (Tutin, 1938). This suggests that dispersal is not very effective.

(i) *Viability*. The viability of the seeds was determined in the same way as for *Z. marina*. In daylight at 16° C. 8% germinated between November and February; in daylight at 9–13° C. 38% germinated, all in March and April and in the dark at 12–15° C. 40% germinated between January and April, mostly in the last two months. From this it seems that germination is always higher than in *Z. marina* under the same conditions.

(j) *Conditions for germination*. It seems from the above that germination occurs indifferently in the light or dark.

(k) *Morphology of seedlings*. See *Z. marina* (Fig. 2).

(l) *Relative importance of reproduction vegetatively and by seed*. Vegetative reproduction probably results in wider dispersal, but is less important than in *Z. marina*.

IX. *Parasites: diseases*. *Labyrinthula* was apparently responsible for the death of a small patch in the R. Tamar. No other parasites recorded.

X. *History*. No information.

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## BRITISH ECOLOGICAL SOCIETY

### ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, OXFORD

3-5 JANUARY 1942

#### *Saturday, 3 January*

The winter meeting of the Society was opened at 8.45 p.m., on Saturday, 3 January, in the University Department of Botany, Oxford. The evening was chiefly a social gathering of members and guests, of whom about fifty were present. During the evening Prof. H. G. Champion gave an admirably illustrated lecture upon 'Biotic influences in the temperate Himalayas'. He described the forest zones in the Western Himalayas near Dehra Dun and Nainatal, with the altitudinal sequence of *Shorea*, *Pinus* and *Quercus* forests, *Pinus excelsa* forest replacing the oak as the uppermost forest belt in the north-west. Among the biotic effects described were: (a) suppression of regeneration by the grazing of wild animals in sub-montane regions; (b) ancient terraced cultivation, traces of which can still be seen in the pine forests; (c) annual burning of the forest floor to obtain early grass, a practice leading to suppression of shrub growth and all regeneration, as well as soil destruction and restriction of the trees to a few resistant species; (d) the constant lopping of boughs of the oaks for feeding the foliage to buffalo and goats; (e) grazing by buffalo, sheep and goats often of such intensity as to cover the hillsides with a close network of animal tracks, exposing bare ground and causing erosion and landslips, and a highly selected residual vegetation of plants such as species of *Berberis* and *Cotoneaster*.

During the evening Mrs Osborn provided extremely generous refreshments for the meeting, which finally closed about 11.30 p.m.

#### *Sunday, 4 January*

At 10.0 a.m. on 4 January the meeting continued by the giving by Mr C. Diver of his Presidential Address on 'The Limits of Tolerance'. Departing from custom in view of the special circumstances of the meeting and of the President's wish, there followed an interesting discussion of the ideas he had put forward. In this discussion Mr Elton, Dr Blackman, Dr Turrill, Dr Watt, Dr Godwin and Mrs Harvey took part.

The business meeting of the Society was then opened by the reading and signing of the minutes of last year's Annual Meeting. The following new members were elected: N. F. J. Hamblin (proposed C. Elton), Dr Marie Rosenberg (proposed P. W. Richards), J. H. Burnett (proposed A. R. Clapham), Mrs H. Moore (proposed V. S. Summerhayes), J. S. Watson (proposed H. N. Southern).

The report of the Hon. Secretaries of the work of the Society in 1941 was accepted in the form already approved by the Council.

#### *Hon. Secretary's Report for the year 1941*

The twenty-seventh Annual Meeting of the Society was held in the Botany School, Cambridge, on Wednesday, 8 January 1941. On the evening before this the Master and Fellows of Clare College had allowed the use of their beautiful Combination Room for a soirée which was attended by about sixty members and guests. During the evening Mr Frank Kendon demonstrated the great potentialities of colour photography by showing a series of most beautiful lantern-slide portraits of wild plants. After conclusion of the business on the Wednesday morning, the Annual Meeting listened to a series of interesting short papers covering different aspects of plant and animal ecology. The Society is much

indebted to Prof. Brooks for extending the hospitality of his Department to them and for defraying the costs of the soirée, and to the Cambridge Botany School members for their help with the meeting.

As in 1940 arrangements were made to hold a summer meeting, but the uncertainties of the times led to a small provisional acceptance by members, and the meeting was cancelled. We are sorry to have caused Prof. Osborn and his colleagues the trouble of arranging this meeting, and feel on that account especially pleased to be holding the next Annual Meeting with them in Oxford.

Throughout the year Council Meetings have been held in the rooms of the Linnean Society, a convenient facility for which we are very grateful to the Council of the Linnean Society.

During the past year two numbers of volume ten of *The Journal of Animal Ecology* have been published, appearing in May and December, and containing respectively 174 and 202 pages. Fifteen original papers, with nine plates, in addition to reviews, the Society's notices, and the notices of publications on Animal Ecology. In his task of editing the *Journal* Mr Elton has had the continuous and valuable assistance of Mr D. Chitty.

Two numbers of *The Journal of Ecology* have appeared, the first in March, and the second, delayed by printing and publishing difficulties, not until November. They contained respectively 192 and 200 pages and included eighteen original papers with twenty-two plates, as well as notices, reviews and the four first accounts of the Biological Flora of the British Isles. It has been very gratifying to find the *Journals* able, despite the war, to maintain themselves satisfactorily.

During the year the Society has put into effect the instruction of the Annual Meeting of 1940 to initiate publication of a Biological Flora. The Council empowered an *ad hoc* committee of three, the Editor of *The Journal of Ecology*, Dr A. R. Clapham and Dr P. W. Richards, to organize preparation of accounts of selected plant species upon an approved plan, and the first accounts, dealing with four species of *Juncus*, have already appeared. These and the succeeding accounts as they appear in *The Journal of Ecology* are to be printed off, and made available for separate purchase.

Delegates from the Council of the Society have co-operated with representatives from the Society for Experimental Biology and the Association of Applied Biologists, and have succeeded in getting established a national 'Biology War Committee', through which much closer contact can be made between biologists and the Government. This committee has already been at work and has successfully passed on some recommendations collected from members of this Society by questionnaire. At the request of the Biology War Committee, members of the Society have co-operated in the collection of hips from named species of rose and other fruits growing in different parts of the country: these have been used for the determination of vitamin C content.

During the year the membership of the Society has risen from 335 to 363 members, 8 members having resigned or died, and 36 new members having been elected. Of the present membership list 195 receive *The Journal of Ecology* alone, 117 *The Journal of Animal Ecology* alone, 49 take both *Journals* and 2 neither.

In the early part of the year the society lost by death Mr Hugh Boyd Watt, who for many years so faithfully and ably served them as Honorary Treasurer. Later in the year we were shocked to hear of the sudden death of Sir A. W. Hill. The Council of the Society feels that the support given to the launching of the new Flora, the response to circularized requests for information and the increased membership indicate that they can count on every co-operation by members in maintaining the activities of the Society as fully as war conditions will allow.

It was agreed that Dr H. Godwin, already a member of the Biology War Committee, should represent the Society on that body.

Mr V. S. Summerhayes then gave a provisional statement on behalf of the two Hon. Treasurers of the financial position of the Society, and the meeting was pleased to learn that despite war conditions a favourable balance for the year could be counted upon with certainty, thanks to a generous grant by the Royal Society for the purpose of maintaining our scientific journals. The meeting accepted the proposal of Mr Summerhayes that a grant of £10 should be made to the Fresh Water Biological Association in 1942. The thanks of the Society were given unanimously to the Hon. Treasurers for their industrious and successful efforts, and in reply Dr Watt suggested that members could lighten these efforts by still greater use of Banker's Orders in paying subscriptions. On the proposal of Mr Harvey, Messrs William Norman and Sons were reappointed auditors to the Society.

Officers of the Society were then elected as follows:

*President*: H. GODWIN.

*Vice-Presidents*: C. DIVER, A. R. CLAPHAM.

*Hon. Treasurers*: V. S. SUMMERHAYES, A. S. WATT.

*Hon. Editor of The Journal of Ecology*: W. H. PEARSALL.

*Hon. Editor of The Journal of Animal Ecology*: C. ELTON.

*Hon. Secretaries*: H. GODWIN, A. L. HARVEY.

*Ordinary Council Members*: D. H. CHITTY, F. T. K. PENTELOW, P. W. RICHARDS, J.

RITCHIE, W. B. TURRILL, V. CONWAY, H. N. SOUTHERN.

[*Retiring Council Members*: E. J. SALISBURY, G. H. BATES, E. W. JONES, A. D. MIDDLETON, T. T. MACAN, G. C. VARLEY, J. S. L. GILMOUR, A. R. CLAPHAM.]

In making the above elections it was agreed that Dr Godwin should continue to perform such secretarial duties as do not conflict with those of President.

Finally Dr G. E. Blackman reported to the Society on the origin and mechanism of the Biology War Committee, indicating that it has already been the means of implementing one important proposal originally put forward by the Society.

#### *Afternoon Excursion*

The afternoon was spent in an extremely pleasant visit to Bagley Wood on the outskirts of Oxford, under the leadership of Dr E. W. Jones, who with Prof. Champion, Mr Foggie and Dr Clapham were able to point out the main features of ecological and forestry interest. The wood, which is mainly on Kimmeridge Clay, showed the difficulty of managing heavy clay soils as forest land, for on the clay the oaks (*Quercus robur*), and to a less extent the ashes (*Fraxinus excelsior*), were small and stunted, whilst showing better growth on sites capped with gravel. A great deal of the wood represented very old and feeble oak (hazel) coppice, so dense and so choked with shrubs as to present the most serious problems in any attempt to establish good forest cover. Throughout the wood local effects of soil variability were clearly evident, as for instance in the distribution of rushes, alder and sallows along seepage lines, and the varying quality of tree growth on lighter or heavier clay soils.

#### *Evening Meeting*

At 8.45 p.m. in the evening the meeting was resumed in the Department of Botany and members were able to examine at leisure an interesting series of exhibits illustrating different aspects of plant and animal ecology, especially those concerning the new Biological Flora. During the evening some of the contributors gave short talks upon the material of their exhibits. These were (a) Mr J. P. M. Brennan, who said that many, at any rate, of the recently described British species of *Euphrasia* appear ecologically as well as morphologically distinct. The range of habitat was briefly described for fourteen species; some, however, were still insufficiently known. It appeared that ecological isolation has been an important

factor in evolution within the genus. (b) Mr F. Ballard, who gave a general account of cleistogamy in grasses, which is appended to this report together with a summary of the remarks of the next speaker, (c) Mr C. E. Hubbard, upon his exhibit of the collective species *Glyceria fluitans*. (d) Dr J. Fisher explained how the British Trust for Ornithology had had the co-operation of the Coastal Command of the R.A.F. in securing a series of beautiful and accurate photographs of the bird cliffs round the north British coast, including Rockall, St Kilda, Ailsa Craig, Little Skellig, Grassholm and the Flannan Isles. In many instances these gave very good evidence of the kind and amount of bird life present, so affording valuable checks upon changes since the surveys of recent expeditions.

Other exhibits were those of: (e) Dr Turrill, who exhibited herbarium specimens to show the large range of variation in *Senecio squalidus* (the Oxford ragwort), which could be found within the confines of a single garden. Variation in leaf form and size, in size of florets and capitula, hairiness of cypselas, and branching habit were evident, and as the species is now spreading rapidly the desirability of studying its variation is apparent. (f) Dr Polunin, who showed herbarium specimens of *Carex praticola* Rydb. from Viking ruins in South-west Greenland and suggested that this was a species possibly introduced from America by man. He also put out specimens of the North American species *Carex bicolor* from North America and from the Inner Hebrides. (g) Mr Elton, who put out an exhibit of journals and other publications from the U.S.A., showed how the generous output of officially sponsored scientific literature on wild-life conservation and survey in that country contrasts with our own meagre output. (h) The Bureau of Animal Population, which showed experimental methods developed in their work on rodent control, the first the permanent poison point (P3) used in the pre-baiting technique of exterminating rats, the second the method of dyeing food offered to rats so as to trace their movement by means of the variously coloured excreta, and the third an automatic device for measuring rabbit activity. Examples were also shown of sheaves and grain from stacks badly infested by rats and mice.

The meeting dispersed at about 11 p.m.

*Monday, 5 January.* At 10.0 a.m. the meeting reopened with a paper by Mr D. CHITTY on 'The Feeding behaviour of wild brown rats'. He outlined the difficulties of tracing the movements and of estimating the size of populations of these rodents, and very competently and dramatically illustrated how by regular feeding the full rat population of a locality could be brought to feed at a given point where it could be reckoned to eat 1 oz. of wheat per rat each night. In the stimulating discussion which followed Dr Jones, Mr Harvey, Dr Blackman, Dr O. W. Richards, Mr Elton, Mr Summerhayes, Dr Watson, Dr Watt, Mrs Harvey, Mr Middleton, Dr Godwin, Dr Turrill and Mr Hughes took part, and many interesting features of rat behaviour were touched upon. Dr A. R. CLAPHAM then followed with an account of *Galium uliginosum* and forms of *G. palustre*. *G. uliginosum*, a clearly distinct species with chromosome number  $2n=22$ , was characteristic of calcareous fens and peaty alluvia. There was a large octoploid ( $2n=96$ ) form of *G. palustre* growing chiefly in shallow standing water with *Magnocariceta* or *Alnus-Frangula-Salix* fen scrub; a small stiff form of *G. palustre* ( $2n=24$ ) found in meadow habitats wet but liable to drying-out in summer, and a rarer intermediate form with  $2n=48$  chromosomes. Dr Clapham also considered briefly the distinct and restricted species *G. debile* ( $2n=24$ ) with typical long submerged linear leaves in the winter form. The taxonomic status and operation of the ecological separation of these forms was considered, and it was suggested that the soil aeration was indirectly involved in the habitat separation of *G. uliginosum* and *G. palustre*, possibly through some factor such as soil nitrification. Following the paper Drs Turrill and Polunin asked questions of the lecturer.

Dr G. E. BLACKMAN next proceeded to describe his experimental work on the ecology of the bluebell, *Scilla non-scripta*. Measurements of weight of bulbs planted in grassland showed big seasonal effects, those in 1939 trebling in weight and those in 1940 not increasing.

The addition of nitrogen by favouring grass growth and increasing competition caused an actual loss in bulb weight in 1940. Larger bulbs were shown to have a bigger proportional increase in weight than small ones. Further experiments showed that cutting at or just before flowering led to considerable loss of bulb weight, and trampling at these times had similar effects, which were most marked if the trampling took place just before flowering. It was strikingly shown in these experiments that the results could be greatly affected by the strain of bluebell used, those from oak and ash woods respectively leafing at different times and being differently affected by trampling. It was shown by photosynthesis experiments that the compensation point for bluebell leaves was about 8 per cent of total daylight, a figure corresponding with the lower limit of light intensity tolerated by the plant in woodland growth. In the subsequent discussion Dr Jones, Dr Turrill, Mr Tutin, Dr Clapham, Mr Elton, Dr Watt, Dr Polunin and Mr Hughes took part.

When the meeting was continued in the afternoon Dr A. C. HOYLE gave an account of the results of an expedition to the Sudan. After a general description of the great vegetation belts of semi-desert, thorn-woodland and savannah which form a series in passing southwards to regions of increasing rainfall, the speaker described in some detail the various modifications of savannah woodland found in excursions round Wau. The long dry season, grass fires, and the use of axe and fire in farming were given as major ecological factors, and it was shown how these favour soil erosion, which makes much differentiation of modified soil types carrying different vegetation. By lantern slides Dr Hoyle was able to convey a vivid picture of the vegetation described. Dr Morison, who had organized and led the expedition, then gave the society a concise exposition of his views on the relationships of soil, climate and vegetation in this region, stressing the extent to which local soil and vegetation differences are caused by edaphic conditions which affect the fate of the water supply. The general discussion which followed turned upon the importance of termite mounds: Dr Hora, Dr Blackman, Dr Polunin, Mr Foglie, Dr Hale Carpenter, Mr Tutin, Prof. Osborn and Dr Hope Simpson took part.

Dr E. W. JONES then gave a description of work done by Mr Foglie and himself on the regeneration of Douglas Fir in the New Forest, Hampshire. The enclosure and planting of strips of Douglas Fir in 1864 had now produced parent trees 120 ft. high, and copious regeneration in a belt up to  $\frac{1}{2}$  mile away from the parent trees. This regeneration was excellent under *Pinus sylvestris* on loamy, base-deficient degraded soils, but poor under *Quercus robur* on clay soils. It was absent under the dense shade of the parent trees. A careful study of transects established the following points: there is evidence for strong fluctuation from year to year in seed-production, and only about 30 per cent of trees produce cones: in individual sapling groups the colonization period has been very restricted: good seedling establishment occurs in a carpet of moss and bare litter over raw humus and pine needles at a critical stage of opening of the pine wood canopy. Later *Rubus* and *Molinia* invade and conditions become unfavourable again. Dr Jones considered the pine needle litter as of great importance and this raised comment in the following discussion, in which Drs Watt, Godwin and Polunin took part.

The meeting closed at about 4.30 p.m., the President having expressed on behalf of the Society sincere gratitude to Prof. and Mrs Osborn, and their colleagues in the departments of Botany, Zoology and Forestry for organizing the meeting so successfully and to the Societies of Magdalen College and St Hilda's College for their generosity in having provided accommodation for members.

## APPENDIX. ACCOUNTS OF EXHIBITS AT THE OXFORD MEETING

1. *Cleistogamy in Grasses*, by F. BALLARD

Cleistogamy is a widely spread phenomenon in the Gramineae and occurs in more than fifty genera scattered through fourteen of the twenty-seven tribes of the family. It has been known from very early times.

The dry habitats of many cleistogamic species suggests that cleistogamy is connected with water supply, while in a few cases its occurrence is probably due to the low temperature prevailing at flowering time.

Where cleistogamy occurs, the lemma (flowering glume) and palea remain closed during anthesis; the anthers are small; the pollen grains frequently few. The staminal filaments usually fail to elongate and the anthers become carried upwards by the developing caryopsis, being entangled in the stigmatic hairs. The lodicules are very thin and often rudimentary or sometimes suppressed altogether. It has been suggested that the poor development of lodicules is a contributory cause of cleistogamy.

Cleistogamic species may be conveniently classified as follows:

1. *All inflorescences bearing cleistogamous spikelets*. In this group the inflorescences are exserted though pollination usually takes place while still in the leaf-sheath. Examples shown were *Eragrostis pilosa* Beauv.; *Bromus unioloides* H.B. & K. Many others are known.

2. *Inflorescences with cleistogamous or chasmogamous spikelets*. Favourable climatic conditions induce production of chasmogamous spikelets whereas less favourable conditions encourage development of cleistogamous spikelets. Examples shown were *Panicum clandestinum* L. and *Leersia oryzoides* Sw.

The latter species occurs in a few localities in South England. In Britain the inflorescence usually remains enclosed within the leaf-sheath, the florets being cleistogamous. Only in very warm seasons are panicles properly exserted, and in most cases the spikelets, being already pollinated, drop at an early stage. On rare occasions, however, chasmogamous spikelets are produced on exserted inflorescences and investigation tends to show that their appearance coincides with long warm summers. Particularly fine panicles were produced in 1859, said to be the hottest summer for seventy years. During that year maximum temperatures of 79° and 77° F. were recorded for April and May respectively, and it is suggested that such high temperatures at an early stage are conducive to the development of chasmogamous spikelets. Warm seasons which are late in starting may cause the production of exserted panicles, but the spikelets tend to be cleistogamous. The growing of Leersia under controlled conditions should prove of interest.

3. *Cleistogamous spikelets borne in the axils of the leaf-sheaths*. The spikelets may be borne in small inflorescences or solitary, either at all nodes of the culm or only at the basal one. Dispersal is affected by disarticulation of the culms at the nodes (*Calyptochloa*) or by the leaf-sheaths being pushed aside (*Cleistochloa*) or by disarticulating from the culm. Examples shown were *Paratheria prostrata* Griseb.; *Cleistochloa subjunccea* C. E. Hubbard; *Calyptochloa* C. E. Hubbard; *Sieglungia decumbens* Bernh. The last mentioned occurs in Britain. The terminal panicles seem always to be cleistogamous although chasmogamous individuals have been recorded. In addition, solitary sessile cleistogamous spikelets are often found in the axils of the basal leaf-sheaths. These 'cleistogenes' occur also in several species of *Dactyloa* with which genus *Sieglungia* is almost certainly congeneric.

4. *Cleistogamous spikelets on subterranean branches*. These branches are produced at the base of the culm or lower nodes and bear scale-leaves and 'cleistogenes' at their tips.

Examples shown were *Chloris chloridea* Hitchc. and *Amphicarpon Purshii* Kunth. The spikelets on the aerial panicles are perfect but rarely develop caryopses. Fertile caryopses arise from cleistogamous spikelets produced on subterranean branches. These 'cleistogenes' are very turgid and are much larger than the aerial spikelets.

F. B.

## 2. The collective species *Glyceria fluitans*, by C. E. HUBBARD

The collective species *Glyceria fluitans* of many of our British floras and plant lists comprises three comparatively well-defined species, *G. fluitans* (L.) R.Br., *G. declinata* Bréb., and *G. plicata* Fries, and at least one putative hybrid, *G. pedicellata* Towns. The three species are widely distributed in the British Isles, although the first two appear to be more abundant than *G. plicata*. Specimens of *G. pedicellata* (? *G. fluitans* × *G. plicata*) have been seen from many English counties, including Cornwall and Northumberland; it occurs also in Scotland. These grasses, commonly known as Manna Grasses, are semiaquatic perennials, inhabiting wet and muddy places, such as shallow ponds, ditches and slow-running streams, or the margins of rivers and deeper waters. They may occur in adjacent low-lying grassland which in certain seasons is subject to flooding. Although preferring open situations, *G. fluitans* and *G. plicata* are fairly tolerant of shade, but *G. declinata*, while sometimes partially shaded by larger aquatics, is usually found in unshaded places. *G. fluitans* and *G. plicata* are able to grow in the relatively deeper parts of ponds and prefer deep heavy soils rich in humus, *G. declinata* on the other hand is usually confined to the shallow water of pond-margins or the surrounding low muddy ground. The hybrid *G. pedicellata* often occurs in running water and in such situations may become the dominant grass. *G. fluitans* and *G. declinata* tolerate a wide range of soils, varying from the acid sandy soils of drainage ditches in wet heaths to ponds on chalk downs or slightly brackish streams near the sea. All the members of the *G. fluitans* group are associated with common British aquatics, and especially the grasses *Alopecurus geniculatus* and *Agrostis stolonifera* var. *palustris*. In some ponds subject to drying-out in years of low rainfall, the dominant *G. fluitans* of wet years may be almost replaced by *Alopecurus geniculatus* and other plants. The Manna Grasses produce a large amount of palatable herbage which is readily grazed by horses, cattle and sheep; the young leaves are also eaten by water fowl. Agricultural writers point out that there are few grasses better adapted to irrigated ground or land liable to flooding, where grazing would be limited to dry seasons of the year when the turf permits of treading by cattle and when other grasses are in short supply or unavailable. The caryopses, which are edible and relatively large, are sought after by water fowl and reputed to be eaten by fish. Propagation is effected either by detachment of rooted portions of the plants, or by means of seed which is produced in abundance. The seeds are boat-shaped and float for a few days before sinking. Dispersal is also accomplished by the seeds becoming attached to the bodies of water fowl or to the feet of grazing animals. The few varieties recorded are mostly based on plants growing under unfavourable conditions. For example, when competition from other plants is severe, those of *Glyceria* spp. so affected develop simple spike-like inflorescences, which in the case of *G. fluitans* have been given the name of var. *triticea* Fries. The chromosomes in British material of the three species have been studied by Miss Maude, the somatic number being 10 for *G. declinata* and 20 for *G. fluitans* and *G. plicata*. They are much smaller than those of *G. maritima* (Huds.) Mert. & Koch ( $2n=63$ ), now placed in the genus *Puccinellia*.

C. E. H.

## LIST OF MEMBERS (1 FEBRUARY 1942)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

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### *Income*

	£ s. d.	£ s. d.	£ s. d.	£ s. d.
Subscriptions received, including arrears, and less				
Payments in advance:				
Members taking <i>Journal of Ecology</i> only ...	221 2 7			
Members taking <i>Journal of Animal Ecology</i> only ...	144 0 0			
Members taking both Journals ...	103 11 0			
Associate ...	7 6			
Interest on Investments ...	... ...			
Interest on Deposit Account ...	... ...			
Interest—less Expenses ...	... ...			
Grant from Royal Society ...	... ...			
Index volume to <i>Journal of Ecology</i> (vols. I-XX):				
Sales—less Expenses ...	... ...			
Balance (see above, under Expenditure)	... ...			

### *Expenditure*

	£ s. d.	£ s. d.	£ s. d.	£ s. d.
Working Expenses:				
Printing and Stationery	... ...			
Postages	... ...			
Travelling	... ...			
Expenses of Meetings	... ...			
Audit	... ...			
Clerical Assistance	... ...			
Sundries	... ...			
Grant:				
Fresh Water Biological Association ...	... ...			
Biological Flora of the British Isles:				
Cost of Printing Articles, advertising, etc. ...	... ...			
<i>Journal of Ecology</i> . Cost less Sales ...	... ...			
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Balance: Surplus for the Year, carried forward	... ...			
	<b>£674 0 3</b>			
<i>Journal of Ecology</i> , 1941:				
Sales: Current vol. 29 ...	... ...			
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	<b>£654 10 7</b>			
<i>Journal of Animal Ecology</i> , 1941:				
Sales: Current vol. 10 ...	... ...			
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	<b>£592 18 0</b>			

BALANCE SHEET AT 31 DECEMBER 1941

<i>Assets</i>		<i>Liabilities</i>	
Cash at Bank, Current Account	... £ 304 14 7	Members' subscriptions, prepaid for 1942/43	£ 12 5 0
" " Deposit Account	... 400 0 0	Library Fund	1 5 0
Publishing Accounts: Amounts due from Cambridge University Press:	704 14 7	Grant from Burtt-Smynnerton Memorial Appeal Fund	150 0 0
<i>Journal of Ecology.</i> Balance of Account	206 2 8	Balance of Printing Accounts due:	
Index Volume	6 17 10	<i>Journal of Ecology</i> , vol. 28, no. 2	213 15 7
" <i>Journal of Animal Ecology.</i> Balance of Account	106 5 0	<i>Journal of Animal Ecology</i> , vol. 10, no. 2	237 4 3
Stock of Paper in hand	... 318 5 6	Biological Flora of the British Isles	46 4 5
Investments at cost	... 32 19 6	General Revenue Account, Surplus in hand:	497 4 3
	1,268 16 10	Balance at 31 December 1940	1,500 15 0
	<u>£2,324 16 5</u>	Surplus for Year 1941	<u>163 7 2</u>
Notes re Investments:			<u>£2,324 16 5</u>
Cost:	£ 1,050 of 3½% War Loan	£ 1,070 6 10	
	£200 of 5% Conversion Loan	198 10 0	
	<u>£1,268 16 10</u>		
Present-day Market Value of the above Investments:			
3½% War Loan at 105	£ 1,102 10 0		
5% Conversion Loan at 105½	211 10 0		
	<u>£1,314 0 0</u>		

A further Asset, not valued, is the unsold stock of Journals and Index Volumes held by the Publishers for the Society.

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13 February 1942

# THE MARGINAL ALGAE OF CERTAIN PONDS, WITH SPECIAL REFERENCE TO THE BOTTOM DEPOSITS<sup>1</sup>

BY J. W. G. LUND

*(With three Figures in the Text)*

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This investigation was directed to discovering whether there was a definite community of unattached (non-epiphytic) algae living on the bottom deposits of ponds and to determining the influence of these deposits on the littoral algae. Observations have also been made on the planktonic and epiphytic algae of the waters concerned. This investigation was begun in January 1936 and continued until March 1938. A considerable number of the forms encountered are new species or new records for this country. They are fully described elsewhere (Lund, in the press). A complete list of the algae found is given at the end of the paper.

## I. METHODS

Collections were, as a rule, made weekly from all the ponds, and the temperature and hydrogen-ion concentration of the water recorded at each time of collection. Until July 1936, rough determinations of pH were made by using a Universal Indicator, but subsequently records were obtained with a Lovibond Comparator. Calcium deficiency was tested for by using Comber's method as modified by Misra (1938).

<sup>1</sup> From the Department of Botany, Queen Mary College, University of London. The substance of this paper formed part of a thesis approved in 1938 for the Degree of Doctor of Philosophy in the University of London. Fuller details on many of the matters dealt with in the present paper will be found therein.

Approximately 150 ml. of the surface water was taken at each station and subsequently centrifuged in the laboratory; no net collections were made. The majority of the organisms found in the Pen Ponds are nannoplankton, being less than  $30\mu$  in diameter, and would, therefore, pass through the finest bolting silk. Certain algae (*Microcystis aeruginosa*, *Anabaena flos-aquae*, *Volvox*) cannot, however, be obtained in a satisfactory condition by using the centrifuge. For investigation of the plankton, two centrifuge tubes (13 ml. capacity) were filled with some of the water and centrifuged at approximately 2000–2300 r.p.m. for  $2\frac{1}{2}$  min. The application of stronger centrifugal force causes distortion and disintegration of the more delicate forms (e.g. *Chromulina*, *Cryptomonas*, *Synura*) or extrusion of the protoplasts from the envelopes (*Dinobryon* and *Kephryion*). At this speed nearly all the organisms present were concentrated at the bottom of the tube within  $1\frac{1}{2}$  min.; two drops (each of 0.5 ml.) of the well-mixed sediment were placed separately on a slide and covered with cover-slips. The different organisms were then counted in five fields under each cover-slip at a magnification of 400 and three complete transects were also made of each drop and any organisms not previously enumerated were noted as present. A sample of the surface of the bottom deposit was obtained by suction. The apparatus employed consisted of a hand suction pump fitted to one hole of a two-holed rubber bung fitted to a collecting bottle; through the second hole was inserted the arm of a thistle funnel bent twice at right angles. For use the apparatus was lowered gently, so as to cause the minimum of disturbance, until the open mouth of the funnel was in contact with the deposit, the surface of which was sucked up into the bottle by the action of the pump. Meanwhile the mouth of the thistle funnel was allowed to travel slowly over the surface. A certain amount of the overlying water was naturally also sucked up with the sediment. This method is not suitable for obtaining the larger filamentous algae (e.g. *Spirogyra nitida*) which are, however, rarely present on the deposits. With these reservations, the method proved very satisfactory. Wet mud, above the water level, was collected by scraping off with a scalpel sufficient of the surface to fill a small specimen tube ( $2 \times \frac{1}{2}$  in.). Parts of aquatic macrophytes and other substrata occurring in and around the areas under observation were collected once a month for the study of the epiphytic growth. Monthly samples of the bottom deposits, in which the organic matter was determined by incineration, were taken by carefully pressing an open circular tin, having a sharp edge, into the deposit, the tin being slowly twisted so that it cut through the deposit. When full the lid was slid underneath the tin and the latter withdrawn from the deposit. By this means a circular disk, 2 cm. deep and 7.5 cm. in diameter, was cut out.

The samples of the bottom deposit were well shaken and three separate fractions, each of 0.5 ml., were taken. Of two of them three and of the fourth four fields (i.e. ten in all) were examined. Two transects through each made it possible to record any organism not previously enumerated. Since it is not possible, owing to their varying nature, to obtain equivalent amounts of deposit at each collection, and since the amount obtained from two different stations varies with the nature of the deposit, the numerical results both for the same and for different stations are not strictly comparable. The samples from the surface of exposed deposits, after mixing with 10 ml. of distilled water and thoroughly shaking, were examined in the same way as the others.

Only the more abundant bottom-living organisms can be found by these methods, since only very small quantities of the deposits are utilized. In order to obtain further data, samples, after addition of Pyrex distilled water, were left overnight and re-examined next

morning. Such 'one-day' samples, as they may briefly be called, were first started in October 1936. The dishes were painted black except for a small area on the side facing the light. By the following morning the majority of the phototactically sensitive motile forms had aggregated on the illuminated side, while others had moved to the surface of the deposit. As the majority of the bottom-living algae are motile and show more or less marked positive phototaxis, the method is very efficacious for concentrating them within a relatively small space. In examining these cultures six drops (0·3 ml.) were taken from each dish, two from the water and mud surfaces respectively on the illuminated side and two from a spot chosen at random on the surface of the deposit. The relative abundance of the various forms was recorded by means of symbols (see Table 1, p. 256).

While the value of numerical data was fully realized, the time requisite to obtain counts sufficiently large to possess some degree of accuracy made them unfeasible. At first a limited amount of counting was done on field material and, even after its inadequacy had been recognized, it was continued so that all the results might be of a uniform nature. In a preliminary survey of relatively unknown habitats, such as those dealt with in this paper, it was considered to be of greater importance to obtain a general idea of the various types of communities and of their variation in a number of somewhat dissimilar habitats than to make very detailed observations in one single instance.

There are, moreover, a number of factors militating against the accuracy and value of the counting method, particularly as applied to these types of floras. Thus the occurrence of some of the bottom-living algae in clumps, or their movement into certain restricted temporarily favourable areas, renders large-scale counting necessary to obtain correct numerical estimations.

In examining cultures, moreover, the thorough mixing requisite disturbs both deposit and algae and creates artificial conditions affecting the flora, since a relatively thin superficial layer of such deposits—of the greatest importance in relation to the supernatant water—differs markedly in constitution and often in physical structure from the rest, owing to the greater degree of oxidation of the organic matter present. In relation to biological productivity, counts tend to give a false idea of the importance of the smaller forms which can hardly make the same nutritive demands as the larger ones. Marked differences in abundance will be just as apparent by using symbols, which are of course open to criticism, since they are bound to be used with a different scale of values by two different observers and the same observer may not maintain corresponding values over an extended period of time.

Epiphytic forms were killed and preserved in 4% formalin while a 0·5-1% solution of osmic acid was used for the bottom-living and planktonic algae which included many Flagellates. In the case of diatoms the material was strongly boiled in concentrated nitric acid and washed in tap water followed by distilled water. Where small or relatively scarce diatoms were concerned, the material was incinerated on a slide; the position of the specimens was thus known and they could be found after treatment. The material was mounted in Styrax (permanent) or  $\alpha$ -monobromonaphthalene (non-permanent mount).

## II. GENERAL FEATURES OF THE PONDS AND OF THE SURROUNDING LAND

Oak and bracken are the most prominent plants in the area surrounding the ponds. The oak is accompanied by beech, birch, hawthorn and, around the Pen Ponds, alders and willows. The subsoil consists of sand and clay which often run in bands, and the sand is

commonly admixed with gravel. The main gravel areas are now, however, probably occupied by ponds. There is also a certain amount of loam. A large part of it is covered by a thin layer of bracken peat which is very acid ( $pH\ 4.0-5.0$ ). Acidity of the soil is, however, general, and tests made by Comber's method (Misra, 1938) show that it is strongly calcium deficient. The artificial drainage system has probably contributed to the leaching of the soil.

The Upper Pen Pond, which is the largest, is surrounded by several plantations, and is fed by a number of drains. It is separated by a dam from the Lower Pen Pond, which lies several feet lower. An exit drain from the upper allows excess water to overflow into the lower, and this flow is considerable during winter and spring. The Lower Pen Pond is four-sided and is at least in part artificial. The presence of gravel beneath these ponds and the occurrence of a number of gravel pits in the park, suggest that removal of gravel may have played some part in their formation. From the evidence available it seems likely that the two ponds are about 300 years old.

The Leg-of-Mutton Pond also gives the impression of being partially artificial, since it lies at a much higher level than much of the surrounding ground. The small Clay Pit resulted from the extraction of clay some 16 or 17 years ago. A number of much smaller pits lying in the same hollow form temporary pools during the wetter periods of the year. The Clay Pit is not linked with the drainage system of the Park and is altogether stagnant. A single drain feeds the Leg-of-Mutton Pond, and most of the excess water from it passes into the Upper although some flows into the Lower Pen Pond. The Upper and Lower Pen Ponds are fed by a number of drains, originally open watercourses, which are now more or less completely underground. Owing to this extensive drainage system a large volume of water passes into the Upper Pen Pond during the wetter periods of the year, the excess flowing into the Lower Pond and thence to Beverley Brook.

All the ponds are shallow, the Upper Pen Pond alone exceeding 2 m. in depth and in places reaching nearly 4 m. In spite of their close proximity they show considerable differences in the nature of the substrata (cf. p. 277). There are few sources of pollution, but aquatic birds and, especially, surrounding trees, add organic matter to the water.

### III. ALGAL FLORA AND SEASONAL VARIATION<sup>1</sup>

The data summarizing the abundance and frequency of the more important algae are given in Table 1, in which the different areas are listed in descending order according to the organic content of their bottom deposits. The last three columns refer to the exposed deposits occurring in certain areas during the summer. The algae are arranged in four groups: I, filamentous Chlorophyceae; II, bottom forms, chiefly occurring in the Clay Pit and upper littoral of areas C and E; III, bottom forms, chiefly occurring in the lower littoral of areas C and E; IV, planktonic algae. For each group they are generally listed, within their classes, in alphabetical order. The occurrence of each alga in a pond or special area is epitomized by three symbols (from left to right), viz. the greatest abundance attained, the period, months of the year numerically, covered by such abundance, and the number of times the alga occurred in the samples expressed as a percentage of the total possible. Where there is no clear period of maximum abundance, the following abbreviations are used: *Isol.*, sporadic occurrence, or *Var.*, various periods of maximum abund-

<sup>1</sup> Reference should be made to Table 1, p. 256, for details as to abundance, periodicity and occurrence of the algae mentioned in the various ponds.

ance. The species grouped as residue are in general those not listed separately in this table; when they possibly include some already listed, this is indicated by an asterisk (\*). The symbols used are a., abundant; f., frequent; o., occasional; r., rare; v.r., very rare; these and the other features of the table are based on fuller tables contained in a Ph.D. thesis (see p. 245) lodged in the library of the University of London, as well as in that of Queen Mary College, and on other facts obtained from the original samples collected in Richmond Park.

### (i) *The Clay Pit*

The stagnant Clay Pit receives large numbers of dead leaves each autumn from the surrounding *Quercus sessilis*. The edge is occupied by a narrow belt of *Juncus communis*, together with *Hydrocotyle vulgaris* and *Glyceria fluitans*; the last spreads into the shallower water. The central region is covered in summer by floating leaves of *Potamogeton natans*, while *Lemna trisulca* and *L. gibba* occupy the whole surface. A species of *Nitella* is common in the summer, and there are small patches of *Callitricha* sp.

The maximum depth does not exceed a metre. The black bottom deposit, more than 70 cm. deep, consists of clay richly admixed with decomposing oak leaves and branches and remains of aquatic plants. In summer a thin surface film of the mud becomes brown as a result of oxidation, but in winter only the marginal regions show any brown surface; the rest of the mud is strongly reductive in nature and produces large quantities of methane. Hydrogen sulphide could not be detected. The mud is strongly calcium deficient. 29–37·5 % of organic matter is present in the marginal deposits and 46–54 % in the more central regions. In comparing the organic content with that of the other ponds it must be remembered that the deposit of the Clay Pit is mixed with clay and is much the deepest. Its effect on the water, moreover, is greater owing to the stagnant conditions, the relatively small size and the whole of the bottom being composed of this deep organic mud.

The water is opalescent and of a light brown colour which is due to colloidal ferric oxide. Suspended clay particles frequently add materially to the turbidity of the water, as also do maxima of brown-coloured algae such as *Trachelomonas* (especially *T. varians*) and *Synura uvella*. Light penetration is, therefore, small. In very wet weather (February 1937) the pond overflows at its western edge and, during the summer months, areas of bare mud appear at the margins.

The pond was under observation from September 1936 to March 1938, although the central region was only examined from January 1937 to March 1938. The algal flora is, in general, uniform in the marginal and central regions. It shows the following three phases (Fig. 1, Table 1):

(1) From late September to early March flagellates are common and at times very abundant, while epiphytes and *Spirogyra nitida* are infrequent. There are two subphases. From late September to December or January, Euglenineae (esp. *Trachelomonas varians* and its var. *minor*) are dominant, while from January or February to February or March *Synura uvella* is dominant and colours the water, being accompanied by *Mallomonas intermedia* and *M. heterospina* n.sp. The maximum of Euglenineae occurs at the close of the period of leaf-fall, and was greater in 1937 than in 1936. The *Synura uvella* phase occurred earlier and was more marked (December to end of January) in 1937 than in 1936 (late January to March). Species of *Cryptomonas* were most abundant during the second subphase, but their maxima were somewhat irregular.

(2) From March to mid-June flagellates are few, while epiphytes and *Spirogyra nitida* are abundant.

(3) From mid-June to late September flagellates increase somewhat and *Spirogyra nitida* is abundant. Certain other algae are characteristic but scanty, notably *Closterium*

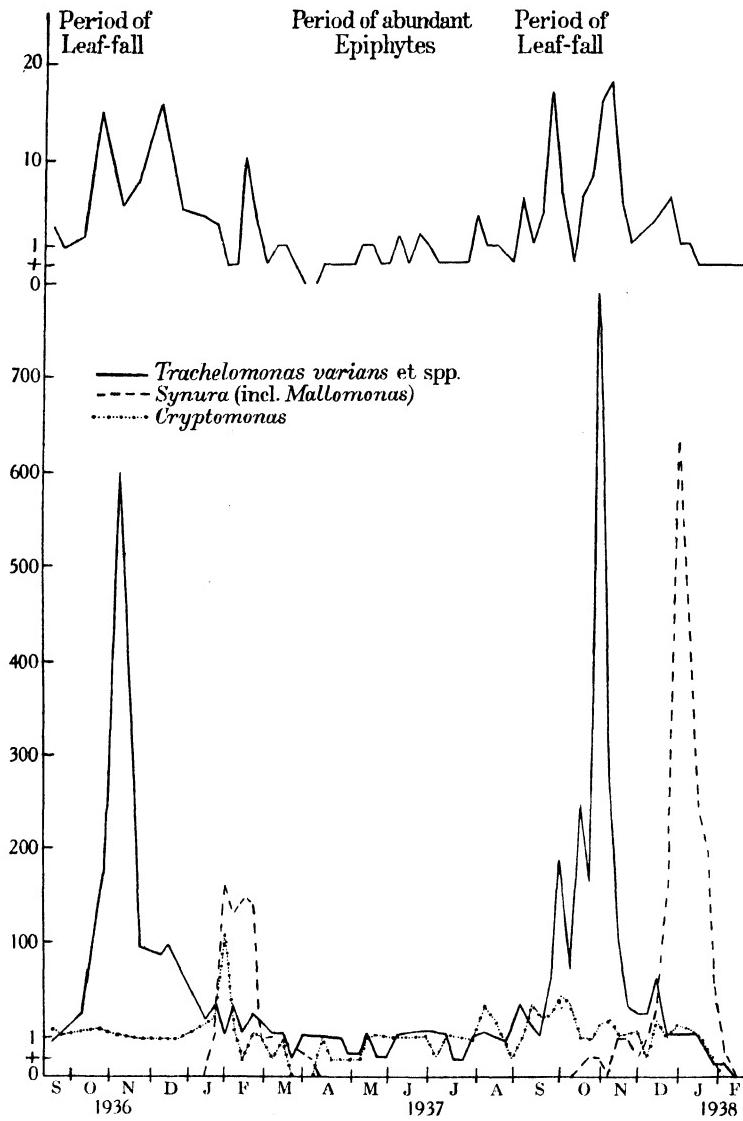


Fig. 1. Seasonal variation of the most abundant algae in the marginal region of the Clay Pit. The top graph represents frequency of species of *Euglena*, *Lepocinclis*, and *Phacus* as a whole; the bottom one that of species of *Trachelomonas* (continuous line) and of *Synura* (*uvelia*, including *Mallomonas heterospina* and *M. intermedia*) (interrupted line); species of *Cryptomonas*, including *Chroomonas Nordstettii* (dotted line).

*venus*, *C. striolatum*, *C. Malvinacearum*, *Volvox aureus*, *V. globator* and a few pennate diatoms. The last are very abundant on the wet mud round the edges.

In the marginal regions in the first subphase the flagellates are distributed throughout the water, although they tend to be commonest in the surface layers, and this greater

preference for the latter is marked in the central regions. During the second subphase the Euglenineae are replaced by Chrysophyceae which are, moreover, much more strictly planktonic. During this phase the bottom flora in the central region is dominated by species of *Phacus* and *Euglena*. The water is acid ( $pH$  6.2-6.9) throughout these two sub-phases and, except around the margins, the surface of the bottom deposit is black.

This subphase lasts about a month and is followed by a period of relative paucity of flagellates. The total algal productivity, however, is certainly no less during the second phase, since epiphytic algae (especially *Tribonema affine*, *Microspora stagnorum*, *Chaetophora elegans*, species of *Synechra* and *Eunotia lunaris*) occur in great quantity. *Spirogyra nitida* occurred abundantly in 1937 in the later part of this phase.

During the third phase, when macrophytes are abundant and much of the surface is covered by *Potamogeton natans* and the duckweeds, the water shows a relatively high alkalinity ( $pH$  7.0-8.4). The cause of this change in reaction is unknown, but it is paralleled by what occurs in the littoral regions of the Pen Ponds. The  $pH$  tends to be higher in the central than in the marginal regions. The temperatures of the water are, owing to the shade of the trees, not so high as in other habitats. The surface of the bottom deposit is now brown in both regions. Epiphytes are less numerous, but flagellates show an increase. Some of the diatoms abundant on the damp mud are also found on the bottom deposits, notably *Navicula pupula*, *Nitzschia palea*, *Pinnularia viridis*, *Stauroneis phoenicentron* and *S. anceps f. gracilis*. A number of diatoms and species of *Closterium* (see p. 250), especially *Nitzschia palea* and *Closterium venus*, together with some *Anabaena oscillarioides*, occur also in the plankton, being derived from the epiphytes on the leaves of aquatic macrophytes. In the summer the pond level falls so that patches of mud appear above the surface. Moreover, the level of the bottom deposit tends to be raised slightly at this time, owing to the decay of the oak leaves and the production of much humus. Cultures (p. 267) show clearly that the volume of the mud increases during this period. The exposed surface of the deposit consists in large part of fine brownish matter, while the mud below is black; for most of the time it is saturated with water, owing to the great water-holding capacity of the mixture of clay and humus. By September, however, the surface of the mud area began to dry at its edge, and this was followed by an immediate and marked decrease in the algal flora and the appearance of *Vaucheria* (Table 1, col. 1).

The flora of the exposed deposit is dominated by *Oscillatoria tenuis*, which forms large blue-green patches on the mud: it is accompanied by *Anabaena oscillarioides* and species of *Phormidium*. Diatoms are very abundant, and the brown colour of the surface is probably, in part at least, due to them; the commonest species are *Nitzschia palea*, *Navicula cryptocephala*, *N. pupula*, *Pinnularia mesolepta*, *P. maior*, *P. viridis* and *Stauroneis phoenicentron*; *S. anceps f. gracilis* was confined to this pond. Characteristic desmids are *Closterium striolatum* and *C. Malvinaceum*, while species of *Trachelomonas* are uncommon in contrast to their frequency in the pond, a feature probably due to the absence of free water and of resting spores. The species of *Euglena* and *Phacus* present are almost without exception not in a free-swimming state, a few of the former (notably *E. intermedia*, *E. viridis* and *E. pisciformis*) creeping over the surface of the mud. After mixing the latter with water and leaving over-night, free-swimming individuals of *Euglena* are common, while those of *Phacus* are less frequent. Species of *Cryptomonas* are completely lacking. Some of the smaller species of *Chlamydomonas*, often frequent in the mud, are actively

motile, which suggests that they are able to swim in the film of water occupying the interstices between the mud particles.

The most important features emerging from the study of this and the other ponds are summarized on pp. 265-266.

### (ii) *The Leg-of-Mutton Pond*

The Leg-of-Mutton Pond (2000 sq.m.) is connected with the drainage system of the park by a single underground open land drain emerging from a covered reservoir and entering the north-western end of the pond. The opening of the exit drain lies above the level of the surrounding land. The pond is about 1½ m. deep in the centre, which is occupied by *Potamogeton natans*. At the end where the entrance drain is situated, *Juncus articulatus*, *Equisetum limosum* and *Scirpus fluviatilis* form a large bed extending, in summer, into the central region. *Scirpus palustris* and *Littorella uniflora* are also present. The margin of the pond is occupied by *Juncus articulatus* and a little *J. communis*. There are relatively few trees nearby.

The bottom deposit near the entrance drain (including area A), up to 40 cm. in thickness, consists principally of silt from the inflowing water mixed with the remains of *Juncus*, bracken litter and *Equisetum limosum* stems. Over the rest of the pond the comparatively (up to 10 cm. in the marginal region) shallow deposit overlies sand and consists in the main of remains of *Juncus*, bracken litter and other vegetable detritus, together with more or less silt, the quantity depending on the distance from the current flowing through the pond. Dead leaves play no important part in the formation of the deposit. A marginal area in each zone (areas A and B) was chosen for study. From January 1937 to March 1938 the surface algae of the central regions were examined fortnightly. The bottom algae of these deeper regions were only occasionally studied in view of their similarity, especially to area B. Epiphytic algae were collected once a month from the plants surrounding each area.

Area A does not lie in the direct line of flow of the drainage water and is screened from the rest of the pond by the bed of macrophytes. The water has a maximum depth of about 30 cm. in winter. The bottom is very flat, so that when the water-level falls a considerable area is exposed. New increments of silt are added whenever there is an inflow from the drain, but during summer this ceases altogether for a time. The deposit is brown at the surface, especially in summer. It is strongly calcium deficient and, although the thin surface layer is oxidized, the black mud below is reductive and contains considerable amounts of methane; the percentage of organic matter is between 6 and 13. The two phases in the algal flora are (Fig. 2) as follows:

(1) From the end of January until July there is a complete lack of phytoplankton, although bottom-living algae are abundant, the dominant forms being flagellates. Epiphytes are scarce until March or April, when *Hormidium subtile* becomes very abundant.

(2) The phytoplankton present from July onwards is sometimes abundant and shows an autumnal maximum of *Dinobryon sertularia*. The bottom-living algae are now represented especially by *Chlamydomonas*, by species of *Cryptomonas* and of Euglenineae and by *Oscillatoria*. When the area becomes isolated there is a great increase in the abundance of flagellates.

During the first phase the water is very acid ( $pH\ 4.2-5.0$ ) and there is a steady inflow from the drain. The dominant bottom-living algae are *Scourfieldia complanata* and

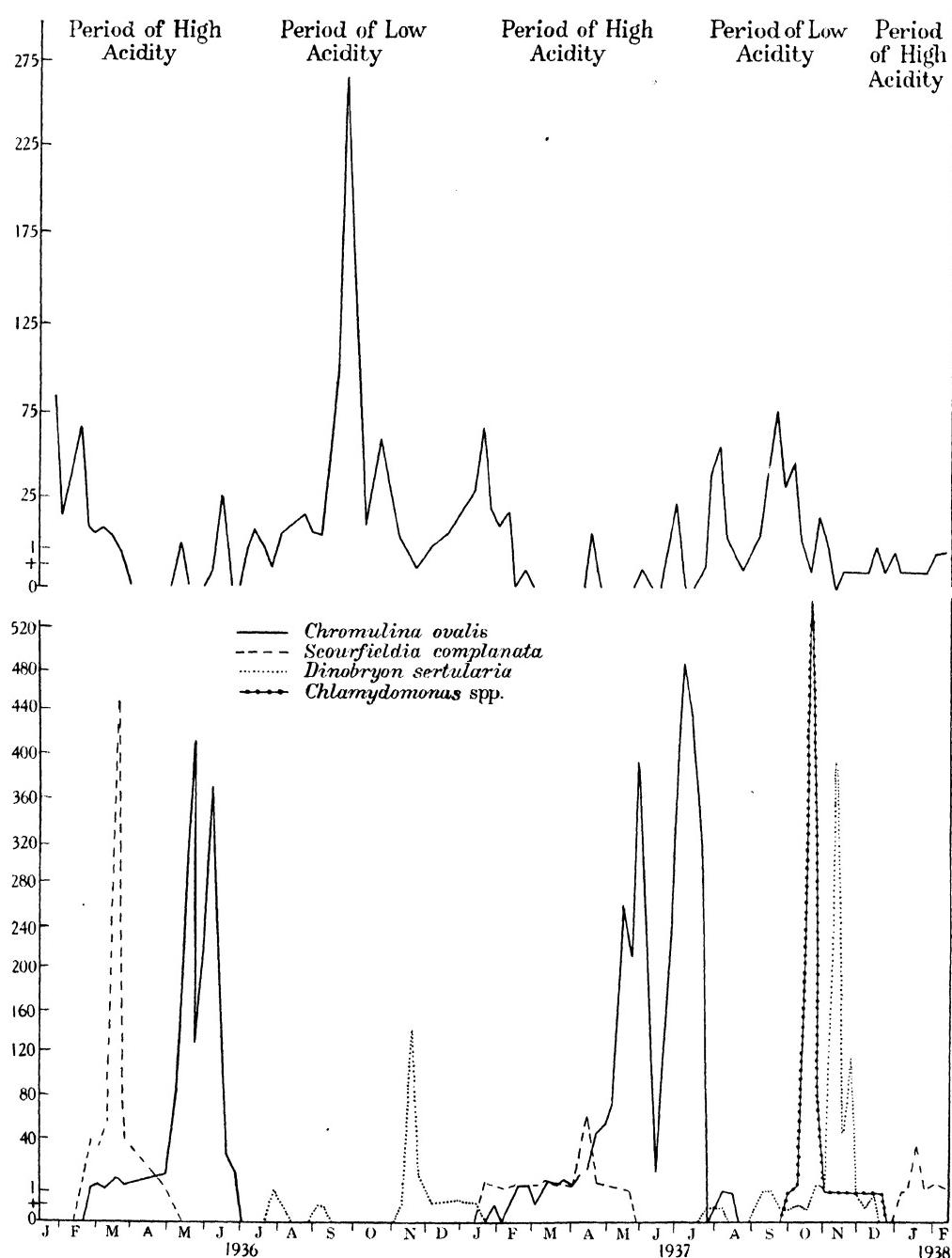


Fig. 2. The Leg-of-Mutton Pond, area A, marginal region. Seasonal variation of the most abundant algae. The top graph represents frequency of species of *Oscillatoria* and the bottom graph of *Scourfieldia complanata*, *Chromulina ovalis*, *Dinobryon sertularia*, including *Chrysococcus rufescens*, and species of *Chlamydomonas* (mainly *C. oblonga*). The frequency of the last named is only given for September 1937 to January 1938, which covers the only period of abundance.

*Chromulina ovalis*, which are frequently present in such immense numbers that, despite their minute size, they form a coloured film over considerable stretches of the deposit. They often surround decaying macrophytes with visible aggregates extending to the surface of the water, although they never accumulate in any open surface water. They are accompanied by *Pseudomallomonas anglica* and *Euglena mutabilis* in much smaller quantities. That these four algae are acid-loving forms is borne out by laboratory observations (p. 274) and occasional collections in other pools in the Park. During March and April *Chromulina sporangifera* n.sp. is abundant among the macrophytes to which it is probably attached for the greater part of its life; the motile stage is sometimes found on the bottom but never in the plankton. *Hormidium subtile* reaches a maximum from May to July and is likewise characteristic of markedly acid water; large mats, consisting almost exclusively of this alga, covering the macrophyte bed and detached pieces floating into the open water. *Scenedesmus longus* and other species of the genus which are present on the bottom in moderate quantity throughout the year also occur around the macrophytes during this period and become detached with the *Hormidium* mats. Numerous chrysophycean spores, probably belonging to *Chromulina sporangifera*, occur during this period (May–July).

The second phase is characterized by a pH of 6·0–6·9 (sometimes over 7·0), and the cessation of the flow of water from the drain occurs about August, though the exact time depends on weather conditions; the period of stagnation may last until October. When the flow starts again, *Dinobryon sertularia* becomes very prominent; at this time the water from the drain is alkaline (pH 7·0–7·3) and only becomes markedly acid at the end of January.

During the second phase bottom-living algae are represented by Euglenineae and species of *Cryptomonas* and *Chlamydomonas* (chiefly *C. oblonga*); they are accompanied by species of *Oscillatoria* (chiefly *O. limosa* and *O. tenuis*) which at times form visible blue-green sheets on the bottom and by a few pennate diatoms (esp. *Pinnularia gibba*). *Bulbochaete subintermedia* is the chief epiphyte. The last fortnight of July and the first of August are characterized by the occurrence of small quantities of Peridineae (*Peridinium*, *Gymnodinium*, *Glenodinium* and a little *Hemidinium*) in the plankton. Though the surface of the deposit is brown there is no swelling, which can be attributed to the lack of readily decomposable leaves, since remains of *Juncus*, bracken and *Equisetum* only disintegrate very slowly. Owing to the flatness of the bottom, large areas of wet mud become simultaneously exposed. This is probably the cause of the absence of a typical exposed mud flora like that found in the Pen Ponds and the Clay Pit (pp. 251, 262, 264). The bare mud in the Leg-of-Mutton Pond is occupied by those bottom-living forms (species of *Oscillatoria* and pennate diatoms) which can exist in the absence of free water.

In 1937, owing to the drier weather, the area became isolated as a separate pool, which showed a rich production of the algae typical for the period (Euglenineae, *Cryptomonas*, *Chlamydomonas* and *Heteromastix angulata*). In October there was only a small puddle less than 1 sq. m. in size and only 1 or 2 cm. deep, coloured green by an intense maximum of *Chlamydomonas oblonga*. With the rise of the water-level in November the area was again united with the rest of the pond and shared the later phases of the very marked *Dinobryon sertularia* maximum; the numbers of *Chlamydomonas oblonga* fell very suddenly.

At the end of January 1938 the water again became pronouncedly acid and the community of Euglenineae, *Cryptomonas*, *Chlamydomonas* and *Chrysococcus* rapidly decreased in importance. The prominence attained by this community, as well as its duration, thus

largely depends on the degree of dryness. Except for *Dinobryon* and *Chrysococcus*, the members are mainly bottom-living forms, though they occur throughout the whole water when the area has shrunk to a puddle.

In the region beyond the plant bed, the flora of the bottom is intermediate between that typical of areas A and B. As in area A, *Chromulina ovalis*, *Scenedesmus longus* and *Hormidium subtile* are absent from the plankton unless the bottom deposit is disturbed. Euglenineae are lacking in the surface waters, except for a brief phase of *Trachelomonas* (November–December 1937) and Peridineae are not well represented. The only abundant plankton form is *Dinobryon sertularia*, which attains a much more pronounced maximum than in area A and is accompanied by a little *Chrysococcus rufescens*.

Area B is situated in the marginal region between the inlet and outlet drains, but outside the flow of the current. It is not screened from the rest of the pond, but beyond it lies the central region with *Potamogeton natans*, and facing it is a small bed of *Scirpus fluviatus* with some *Litorella uniflora*. The banks are steeper, the depth of water close to the edge being about 30 cm. As a consequence, wave action does not so easily affect the bottom deposit which is, also, less mobile than that of area A (see below). Moreover, area B does not face the direction of the prevailing winds (south-west to west), and is bounded at each end by beds of marsh plants.

The deposit, which overlies sand and is up to 8 cm. thick, consists mainly of the remains of *Juncus* and bracken which decay very slowly and of a certain amount of *Equisetum*, *Potamogeton* and *Scirpus* which decay more rapidly. Mixed with these plant remains are fine grey particles of organic matter. Bare patches of sand are occasionally visible, especially in the summer. In the deeper water the deposit is somewhat thicker and contains more of the grey particles, but its flora is very similar. The mud is calcium deficient, but not to a marked extent, and contains only 3–8 % of organic matter.

The flora from the end of January to July is very similar to that of area A, the whole pond at this time being highly acid ( $pH\ 4.2-5.0$ ). There is no phytoplankton, and the bottom-living forms (*Scourfieldia complanata* and *Chromulina ovalis*) are not as abundant as in area A and, consequently, do not colour the deposit to an equal degree. *Scenedesmus longus* is again represented on the bottom throughout the year, but in this area it is the dominant alga with a maximum from July to September. A little *Desmatoxylum bipyramidatum* is always present.

As the inflow of water ceases during the second half of June and July, the  $pH$  rises to above 6.0 and the second phase begins. On occasion the  $pH$  may become neutral or slightly alkaline. The deposit is never exposed and does not become brown. *Dinobryon sertularia* persists longer than in area A and reaches a greater maximum, colouring the water a pale brown in 1937. Species of *Oscillatoria*, *Chlamydomonas* and Euglenineae are absent, which may be correlated with the smaller organic content, the lesser depth of the bottom deposit and other differences. Diatoms like *Pinnularia*, *Nitzschia* and *Navicula* are likewise absent. *Fragilaria construens*, which reaches a maximum between October and March, is much commoner on the bottom throughout the year than in area A, which is probably in part due to the much less frequent disturbance of the deposit.

The epiphytic flora shows about the same series of changes as around area A. Desmids are commoner and may occur sporadically in the plankton and on the bottom during September and October. The more central region opposite area B has just the same bottom and plankton flora, which is not surprising in view of the complete continuity.

*Marginal algae of ponds*

Table 1

	Clay Pit marginal and central regions	Lower Pen Pond (area E) upper littoral	Upper Pen Pond (area C) upper littoral	Leg-of-Mutton Pond	
				Area A	Area B
Organic content of deposit	... 29-54 %	10-33 %	10-28 %	6-13 %	3-8 %
<b>I. Filamentous forms</b>					
<i>Mougeotia</i> sp.	—	r.: 5-8: 24	—	—	—
<i>Spirogyra nitida</i>	a.: 4-5, 9-10: 78	r.: 7: 4	—	—	—
<i>Hormidium subtile</i>	—	—	—	f.: 6: 33	a.: 4-6: 36
<b>II. Bottom-living: Group I</b>					
<i>Desmatractum bipyramidatum</i>	—	—	—	v.r.: Isol.: 1	o.: 5-6: 78
<i>Scenedesmus longus</i> et spp.	—	r.: Var.: 56	o.: Var.: 62	f.: Var.: 100	a.: 1-12: 100
<i>Closterium Leibleinii</i> and <i>C. striolatum</i>	—	v.r.: 6-9: 10	—	—	—
<i>Chromulina ovalis</i>	—	—	—	a.: 4-7: 44	a.: 4-5: 42
<i>C. sporangifera</i>	—	—	—	o.: 2-3: 10	o.: 2-4: 12
<i>Pseudomallomonas anglica</i>	—	—	—	r.: 2-6: 23	r.: 3-6: 16
<i>Scourfieldia complanata</i>	—	—	—	a.: 2-4: 38	o.: 1-4: 36
<i>Chlamydomonas</i> spp.	r.: Gen.: 62	f.: 6-9: 43	v.r.: Var.: 42	a.: 10: 57	r.: Isol.: 22
<i>Volvox</i> spp.	r.: 6-11: 37	r.: 6-7, 9-10: 10	—	—	—
<i>Chromulina ferrea</i>	—	a.: 7-9: 28	v.r.: 7: 18	—	—
<i>Chromulina</i> spp.	r.: 9-12: 30	o.: 4-5: 23	r.: Isol.: 12	r.: Var.: 24	v.r.: Isol.: 7
<i>Mallomonas limnicola</i> and <i>M. radians</i>	—	f.: 10: 34	r.: Isol.: 6	—	—
<i>Ochromallomonas pelophila</i>	—	o.: 10: 34	r.: 7: 8	—	—
<i>Navicula cryptocephala</i>	r.: 6-10: 18	r.: Var.: 18	r.: Var.: 22	v.r.: Isol.: 13	v.r.: Isol.: 2
<i>N. pupula</i>	v.r.: 6-10: 5	v.r.: Isol.: 7	—	—	—
<i>N. rhyncocephala</i>	—	v.r.: Isol.: 9	v.r.: Isol.: 13	—	—
<i>Nitzschia palea</i>	r.: 6-10: 30	r.: Var.: 29	r.: 7-8: 26	v.r.: Isol.: 9	v.r.: Isol.: 1
<i>Pinnularia gibba</i>	v.r.: Isol.: 13	v.r.: Isol.: 4	—	o.: 10-1, 1936: 19	v.r.: Isol.: 2
<i>P. interrupta</i> and <i>P. minutissima</i>	v.r.: Isol.: 2	v.r.: Isol.: 11	—	—	—
<i>P. maior</i>	r.: Isol.: 11	r.: Var.: 35	r.: Isol.: 18	—	—
<i>P. viridis</i>	r.: Isol.: 11	r.: Var.: 41	r.: Var.: 54	—	—
<i>P. mesolepta</i>	—	—	—	r.: Var.: 17	v.r.: Isol.: 1
<i>Stauroneis anceps</i>	v.r.: 7-11: 13	r.: Var.: 26	r.: Var.: 26	v.r.: Isol.: 1	—
<i>S. anceps</i> f. <i>gracilis</i>	—	—	—	—	—
<i>S. phoenicentron</i>	r.: 7-11: 13	v.r.: Isol.: 5	v.r.: Isol.: 6	v.r.: Isol.: 1	—
<i>Chroomonas Nordstetii</i>	v.r.: Isol.: 18	r.: 7, 10: 15	r.: 6-7: 17	v.r.: Isol.: 5	—
<i>Cryptomonas</i> spp.	a.: 1-8: 93	o.f.: 6-9: 80	o.: 10: 61	o.: 10: 26	—
<i>Euglena acus</i>	r.: 11: 19	—	—	—	—
<i>E. caudata</i>	r.: Isol.: 14	—	r.: 5: 7	—	—
<i>E. mutabilis</i>	—	—	v.r.: Isol.: 6	r.: Var.: 29	r.: Isol.: 10
<i>E. pisciformis</i>	r.: Var.: 27	—	r.: 8: 10	—	—
<i>E. tripterus</i>	r.: 8-12: 26	—	r.: 8: 6	—	—
<i>E. spirogyra</i>	v.r.: Isol.: 7	r.: 6-9: 13	v.r.: Isol.: 4	—	—
<i>E. viridis</i>	r.: 10-12: 19	—	r.: 8: 21	—	—
<i>Euglena</i> spp. (residue)	o.-r.: 6-12: 48	r.: Var.: 32	r.: 6-7: 32	—	—
<i>Lepocinclis ovum</i> , <i>L. salina</i> and <i>L. Steinii</i>	f.: 9: 48	r.: 6-9: 14	r.: Isol.: 9*	v.r.: Isol.: 5*	—
<i>Phacus</i> alata	r.: 10-11: 20	v.r.: 6-9: 4	—	—	—
<i>P. caudata</i>	r.: 10-11: 13	—	—	—	—
<i>P. longicauda</i>	r.: 10-11: 30	r.: 6-9: 8	v.r.: Isol.: 2	—	—
<i>P. oscillans</i>	o.: 9-10: 24	r.: Isol.: 7	v.r.: Isol.: 2	—	—
<i>P. pleuronectes</i>	r.: 9-11: 26	r.: 6-9: 11	r.: 6: 8	—	—
<i>P. pyrum</i>	r.: 11-12: 21	r.: 6-9: 20	r.: 5-6: 20	—	—
<i>Phacus</i> spp. (residual)	o.: 11-12: 29	r.: 6-9: 23	r.: 6-7: 15	v.r.: Isol.: 15*	v.r.: Isol.: 7*
<i>Trachelomonas acanthostoma</i>	o.: 10-11: 30	—	—	—	—

Table 1

Exposed deposits (summer)

Lower Pen Pond (area E) lower littoral	Upper Pen Pond (area C) lower littoral	Lower Pen Pond (area F) upper littoral	Upper Pen Pond (area D) upper littoral	Clay Pit	Lower Pen Pond (E)	Upper Pen Pond (C)
2.6-4.3 %	1.3-3.3 %	0.27-0.54 %	0.46-0.53 %			
—	—	o.: 6: 32	r.: Isol.: 10	—	—	—
a.: 8: 57	—	—	—	—	—	—
—	—	—	—	—	—	—
f.: 1-2: 75	o.: Var.: 86	o.: Var.: 54	o.: Var.: 97	—	r.: Var.: 45	r.: Isol.: 18
—	—	—	—	r.: 6-9: 89	v.r.: 6-9: 10	r.: 8: 36
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
v.r.: Isol.: 3	v.r.: Isol.: 5	v.r.: Isol.: 14	r.: Isol.: 32	f.: 6-7: 59	f.: 8: 91	f.: 7-8: 94
—	—	—	—	—	—	—
—	—	—	—	—	r.: 6-7: 45	—
—	—	v.r.: 2-3: 29	v.r.: Isol.: 4	—	—	—
—	—	—	—	—	r.: 6-7: 45	v.r.: 6: 24
—	—	—	—	—	—	—
r.: Isol.: 18	r.: Isol.: 20	v.r.: Isol.: 9	—	f.: Var.: 100	r.: 8-9: 75	r.: 7-9: 59
—	—	—	—	r.: Var.: 59	r.: 8: 9	v.r.: Isol.: 6
o.: 2: 30	r.: Var.: 45	v.r.: Isol.: 5	—	—	r.: 8: 36	—
r.: Var.: 20	r.: Var.: 33	r.: Isol.: 34	r.: Isol.: 37	a.: 6-8: 100	f.: Var.: 82	f.: 7-8: 94
—	—	—	—	—	r.: Var.: 36	—
—	—	—	—	r.: 6-10: 65	o.: 9: 64	r.: Gen.: 82
v.r.: Isol.: 5	v.r.: Isol.: 3	v.r.: Isol.: 3	v.r.: Isol.: 7	r.: 9-11: 35	r.: Isol.: 9	r.: Isol.: 18
v.r.: Isol.: 5	v.r.: Isol.: 5	v.r.: Isol.: 7	r.: Isol.: 11	—	—	—
—	—	—	—	r.: 7-9: 54	—	—
—	—	v.r.: Isol.: 24	v.r.: Isol.: 11	—	—	—
—	—	—	—	v.r.: 6-8: 12	—	—
—	—	v.r.: Isol.: 2	—	f.: 9: 89	r.: Var.: 36	r.: Var.: 24
—	—	v.r.: Isol.: 7	v.r.: Isol.: 7	—	—	—
o.: 7-8: 65 p <sup>1</sup>	r.: Var.: 94 p <sup>1</sup>	r.: Var.: 47	r.: Var.: 43	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
v.r.: Isol.: 3	—	v.r.: Isol.: 2	—	—	—	—
—	—	v.r.: Isol.: 2	v.r.: Isol.: 4	—	—	—
—	—	v.r.: Isol.: 24*	r.: Isol.: 40*	o.: 6-7: 83*	v.r.: Isol.: 36*	v.r.: Isol.: 41*
v.r.: Isol.: 3	—	—	v.r.: Isol.: 4*	r.: Isol.: 18*	v.r.: Isol.: 18*	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
v.r.: Isol.: 5	—	—	—	—	—	—
—	—	—	—	—	—	—
v.r.: Isol.: 5	—	v.r.: Isol.: 3	—	—	—	—
v.r.: Isol.: 3	—	v.r.: Isol.: 3	v.r.: Isol.: 2	—	—	—
—	v.r.: Isol.: 15*	v.r.: Isol.: 2	v.r.: Isol.: 8	v.r.: Isol.: 18*	v.r.: Isol.: 36*	v.r.: Isol.: 18*
—	—	—	—	—	—	—

<sup>1</sup> planktonic

*Marginal algae of ponds*Table 1 (*continued*)

	Organic content deposit	... 29-54 %	Clay Pit marginal and central regions	Lower Pen Pond (area E) upper littoral	Upper Pen Pond (area C) upper littoral	Leg-of-Mutton Pond	
						Area A	Area B
II.	Bottom-living: Group I (continued)						
	<i>Trachelomonas armata</i>		r.: 9-12: 21	r.: 9: 4	—	—	—
	<i>T. abrupta</i>		r.: Isol.: 4	r.: 6, 9: 27	—	—	—
	<i>T. caudata</i>		o.: 10-11: 26	—	—	—	—
	<i>T. hispida</i>		f.-a.: 10: 86	—	r.: 5-6: 23	—	—
	<i>T. intermedia</i>		r.: Isol.: 21	—	—	—	—
	<i>T. varians</i>		a.: 10-12: 93	r.: 4-11: 43	r.: 5-6: 18	—	—
	<i>T. varians f. minor</i>		f.: 9-10: 62	r.: 6-7: 4	—	—	—
	<i>T. volvocina</i>		a.: 10, 1937: 61	r.: 3-11: 51	r.: 5-6: 26	—	—
	<i>Trachelomonas</i> spp. (residual)		r.: 11-12: 32	r.: 5-9: 18	r.: 5-6: 19*	r.: 10-12: 31*	r.: Isol.: 18*
	<i>Anabaena oscillarioides</i>		—	—	—	—	—
	<i>Oscillatoria limosa</i>		—	—	—	f.: 9: 52	v.r.: Isol.: 5
	<i>O. princeps</i>		—	—	—	—	—
	<i>O. splendida</i>		—	—	—	a.: 1-2: 19	—
	<i>O. tenuis</i>	v.r.: Isol.: 15	v.r.: Isol.: 2	o.: 7: 12	a.: 9: 56	v.r.: Isol.: 5	—
III.	Bottom-living: Group II						
	<i>Pediastrum boryanum</i>	—	r.: Isol.: 10	r.: Isol.: 10	—	v.r.: Isol.: 3	—
	<i>Scenedesmus antennatus</i>	—	—	—	—	—	—
	<i>Fragilaria construens</i>	—	o.: Var.: 57	f.: Var.: 53	o.: Var.: 33	a.: Var.: 97	—
	<i>Navicula cuspidata</i>	—	—	—	—	—	—
	<i>Neidium productum</i>	—	—	—	—	—	—
	<i>Nitzschia acuta</i>	—	—	—	—	—	—
	<i>N. dubia</i>	—	—	v.r.: Isol.: 15	—	—	—
	<i>N. flexa</i>	—	v.r.: Isol.: 1	—	—	—	—
	<i>N. recta</i>	—	v.r.: Isol.: 1	—	—	—	—
	<i>N. sigmaeidea</i>	—	v.r.: Isol.: 3	—	—	—	—
	<i>N. vermicularis</i>	—	v.r.: Isol.: 1	—	—	—	—
	<i>N. Tryblionella</i>	—	—	—	—	—	—
	<i>Gyrosigma acuminatum</i>	—	v.r.: Isol.: 7	v.r.: Isol.: 2	—	—	—
	<i>Stauroneis acuta</i>	—	—	—	—	—	—
	<i>Surirella Capronii</i>	—	—	—	—	—	—
	<i>S. robusta</i>	—	v.r.: Isol.: 1	v.r.: Isol.: 1	—	—	—
	<i>Synedra parasitica</i>	—	v.r.: Isol.: 1	—	—	—	—
	<i>Coelosphaerium limnicolum</i>	—	—	v.r.: Isol.: 4	—	—	—
	<i>Holopedium geminatum</i>	—	—	v.r.: Isol.: 1	—	—	—
	<i>Microcystis parasitica</i>	—	—	v.r.: Isol.: 1	—	—	—
	<i>Cymatopleura elliptica</i> and <i>C. solea</i>	—	v.r.: Isol.: 1	—	—	—	—
IV.	Planktonic						
	<i>Ankistrodesmus falcatus</i>	—	r.: 1-2: 24	r.: 2-5: 31	—	—	—
	<i>Pediastrum duplex</i> and <i>P. tetras</i>	—	r.: Isol.: 3	r.: Isol.: 11	—	—	—
	<i>Chrysococcus rufescens</i>	—	a.: 2-4: 67	a.: 2-4: 62	—	—	—
	<i>Dinobryon sertularia</i> and <i>D. divergens</i>	—	o.: 2-4: 20	f.: 3-4: 14	—	—	—
	<i>Kephyrion littorale</i>	—	r.: 2-4: 20	r.: 2-4: 23	—	—	—
	<i>Mallomonas akromonas</i>	—	r.: 2-4: 22	r.: 3: 17	—	—	—
	<i>M. heterospina</i> and <i>M. intermedia</i>	f.: 1-2: 37	—	—	—	—	—
	<i>Synura uvella</i>	a.: 1-3: 24	r.: Isol.: 7	—	—	—	—
	<i>Uroglonopsis americana</i>	—	—	a.: 5, 11-12: 11	—	—	—
	<i>Asterionella formosa</i>	—	r.: 1-3: 15	r.: Var.: 7	—	—	—
	<i>Cyclotella comta</i>	—	r.: 1: 7	r.: Var.: 11	—	—	—
	<i>Cryptomonas C.</i> (var.)	—	r.: 2-4: 24	r.: 2-4: 18	—	—	—
	<i>Anabaena flos-aquae</i>	—	a.: 7: 11	r.: 5: 4	—	—	—

Table 1 (*continued*)

Lower Pen Pond (area E) lower littoral	Upper Pen Pond (area C) lower littoral	Lower Pen Pond (area F) upper littoral	Upper Pen Pond (area D) upper littoral	Exposed deposits (summer)		
				Clay Pit	Lower Pen Pond (E)	Upper Pen Pond (C)
2·6-4·3 %	1·3-3·3 %	0·27-0·54 %	0·46-0·53 %			
—	v.r.: <i>Isol.</i> : 1	v.r.: <i>Isol.</i> : 3	—	—	—	—
v.r.: <i>Isol.</i> : 3	r.: 7: 20	v.r.: <i>Isol.</i> : 9	—	—	—	—
v.r.: <i>Isol.</i> : 5	r.: 7: 14	r.: <i>Isol.</i> : 7	r.: <i>Isol.</i> : 14	—	—	—
v.r.: <i>Isol.</i> : 3	—	—	—	—	—	—
v.r.: <i>Isol.</i> : 5	r.: 6·7: 5	v.r.: <i>Isol.</i> : 3	—	—	—	—
—	—	v.r.: <i>Isol.</i> : 7*	r.: <i>Isol.</i> : 25*	r.: <i>Isol.</i> : 12*	v.r.: <i>Isol.</i> : 9*	v.r.: <i>Isol.</i> : 12*
—	—	o.: 6·8: 24	—	a.: 8·11: 59	a.: 7: 82	f.: 6·7: 69
—	—	—	—	—	—	—
—	—	—	—	—	r.: 7·8: 45	v.r.: 7·8: 35
—	—	v.r.: <i>Isol.</i> : 14	v.r.: <i>Isol.</i> : 4	—	f.: 6·8: 82	a.: 7: 83
—	—	v.r.: <i>Isol.</i> : 9	—	a.: 8·11: 71	a.: 6·7, 9: 91	a.: 6·7: 100
r.: <i>Var.</i> : 30	r.: <i>Var.</i> : 30	r.: <i>Isol.</i> : 16	o.: 7: 58	—	—	—
—	—	r.: <i>Isol.</i> : 7	o.: <i>Var.</i> : 47	—	—	—
a.: 5·3: 100	a.: 5·3: 100	a.: <i>Gen.</i> : 92	f.: <i>Gen.</i> : 88	v.r.: <i>Isol.</i> : 9	r.: <i>Isol.</i> : 35	—
v.r.: <i>Isol.</i> : 18	v.r.: <i>Isol.</i> : 3	—	—	—	—	—
r.: <i>Var.</i> : 30	v.r.: <i>Isol.</i> : 18	v.r.: <i>Isol.</i> : 2	—	—	—	—
f.: 1·2: 15	v.r.: <i>Isol.</i> : 3	—	—	—	—	—
—	f.: 7·9: 90	—	v.r.: <i>Isol.</i> : 4	—	—	—
f.: 1·2: 18	—	r.: <i>Isol.</i> : 19	—	—	—	—
o.: 1·2: 30	—	r.: <i>Isol.</i> : 11	—	—	—	—
o.: 12·2: 30	v.r.: <i>Isol.</i> : 7	v.r.: <i>Isol.</i> : 5	—	—	—	—
—	o.: 8·9: 18	—	—	—	—	—
v.r.: <i>Isol.</i> : 18	v.r.: <i>Isol.</i> : 3	—	—	—	—	—
f.: 1·2: 50	—	r.: <i>Isol.</i> : 30	v.r.: <i>Isol.</i> : 4	—	—	—
r.: 2: 14	—	—	—	—	—	—
o.: 2: 50	—	v.r.: <i>Isol.</i> : 2	—	—	—	—
o.: <i>Var.</i> : 63	r.: <i>Var.</i> : 23	r.: <i>Isol.</i> : 18	v.r.: <i>Isol.</i> : 11	—	—	—
r.: 1·2: 25	v.r.: <i>Isol.</i> : 3	—	—	—	—	—
—	f.: 8·9: 50	v.r.: <i>Isol.</i> : 2	v.r.: <i>Isol.</i> : 4	—	—	—
—	f.: 8·9: 48	v.r.: <i>Isol.</i> : 3	v.r.: <i>Isol.</i> : 4	—	—	—
—	v.r.: <i>Var.</i> : 30	r.: <i>Isol.</i> : 23	r.: <i>Isol.</i> : 23	—	—	—
r.: <i>Var.</i> : 48	—	v.r.: <i>Isol.</i> : 5	v.r.: <i>Isol.</i> : 4	—	—	—
r.: 1·2: 25	r.: 1: 28	r.: 2·3: 27	r.: 4: 37	—	—	—
v.r.: <i>Isol.</i> : 10	v.r.: <i>Isol.</i> : 10	v.r.: <i>Isol.</i> : 3	r.: <i>Isol.</i> : 22	—	—	—
a.: 2·4: 54	a.: 4: 79	a.: 3·5: 54	a.: 3·5: 54	—	—	—
r.: 2·4: 10	o.: 3·4: 18	r.: 2·4: 18	—	—	—	—
r.: 2·5: 18	r.: 3·4: 43	r.: 2·4: 21	r.: 3·4: 40	—	—	—
r.: 2·5: 15	r.: 2·4: 32	o.: 3: 36	o.: 3: 37	—	—	—
—	—	—	—	—	—	—
o.: 4: 3	r.: <i>Isol.</i> : 18	v.r.: <i>Isol.</i> : 5	v.r.: <i>Isol.</i> : 7	—	—	—
—	a.: 11: 18	—	a.: 9: 4	—	—	—
r.: 2·4: 10	r.: 1·2: 4	r.: 2: 11	r.: 2: 11	—	—	—
r.: 1·2: 10	v.r.: <i>Isol.</i> : 3	v.r.: <i>Isol.</i> : 3	r.: 2: 22	—	—	—
r.: 1·3: 42	r.: 1·3: 23	r.: 3·4: 20	r.: 3·4: 24	—	—	—
f.: 6·7: 5	—	—	—	—	—	—

(iii) *The Lower Pen Pond*

The two longer margins of the Lower Pen Pond are bounded by grassland, while groups of trees occur at each end (approximately east and west). Except in the sandy regions, the margins are occupied by *Juncus communis* and *J. articulatus* which extend into the water: *Myriophyllum verticillatum* and a species of *Potamogeton* also occur in the deeper waters of the areas examined. The pond is very shallow (1·5-2 m.), and the depth increases very gradually beyond the marginal regions. Water is received from the Upper Pond as well as from the other drains emptying into it; the amount from the former source is considerable during winter and spring, but decreases to a small trickle in summer, and in a dry year ceases altogether so that the pond becomes 'stagnant'.

Two areas were examined. Area E consists of two zones separated by a narrow group of *Juncus communis*. In the following description the two zones are described as upper littoral and lower littoral; the former is possibly similar to the eulitoral zone of Naumann (1925, p. 2), while the latter corresponds to what is generally called littoral. The upper littoral region is rich in vegetable humus and its decomposition products. Area F is on the side opposite to area E. It is more exposed and its bottom deposit consists of sand admixed with clay derived from the erosion of the bank.

(a) The *upper littoral zone* of area E extends from the margin to the *Juncus* plants some 7 ft. beyond. Its separation from the pond as a whole is similar, though not so effective as that of area A, Leg-of-Mutton Pond. The deposit is largely derived from fallen leaves (see below) and is strongly calcium deficient; the percentage of organic matter varies from 10·3-33 %. There are two well-marked seasonal phases in the algal flora and in the nature of the deposit.

The first lasts approximately from October or November to the end of May. In the late autumn the pond fills up and the *Juncus* dies down. At the same time leaves from the surrounding trees are added, but the absence of protection, the large amount of water in the pond and the frequent rainfall and strong winds, all cause much disturbance of the deposit, so that some of it is carried to other parts of the pond, washed ashore, or covered by sand brought in during stormy weather. The low temperatures as well as the instability of the deposit, moreover, retard decomposition of the leaves and other vegetable detritus present. The deposit is black throughout.

The rich plankton is composed of the same nanoplankton forms as occur over the lower littoral zone. It is dominated by *Chrysococcus rufescens* and includes other Chrysomonadales, such as species of *Mallomonas*, *Kephyrion littorale* and *Dinobryon sertularia*, as well as species of *Cryptomonas*, especially a small form (Lund, in the press). In spring there are occasional Chlorococcales (*Ankistrodesmus falcatus*, species of *Coelastrum*, etc.), while *Cyclotella comta* and *Asterionella formosa* occur in small numbers. The bottom flora, probably owing to the physical and chemical factors described above, is very poor and consists largely of *Pinnularia viridis*, *P. maior*, *Stauroneis anceps* and other diatoms washed in from the adjacent lower littoral area. Flagellates are conspicuously absent.

In the second phase, from the end of May to late September (1936) or late October (1937), according to the dryness of the year, an entirely different algal community is present. In the course of the summer the flow from the drains feeding the pond ceases and stagnant conditions obtain. The growth of the *Juncus* belt constitutes a shelter so that the bottom deposit now remains undisturbed. Moreover, the higher temperatures

accelerate greatly the rate of its decomposition, and it is broken down to a fine mud, rich in humic matter and having a brown surface due to oxidation of the ferrous salts to ferric oxide. The water itself is sometimes slightly opalescent owing to the colloidal ferric oxide present. Below the surface the deposit remains black and contains a certain amount of undecomposed vegetable detritus. Methane bubbles are not produced in the same quantity as in the Clay Pit of area A of the Leg-of-Mutton Pond. During the process of decomposition the deposit swells (see also p. 270), and this, coupled with the lowering of the water-level, results in exposure of more or less of the deposit, in 1937 almost the whole area. Owing to the abundant humus the sediment has a strong water-holding capacity and remains saturated.

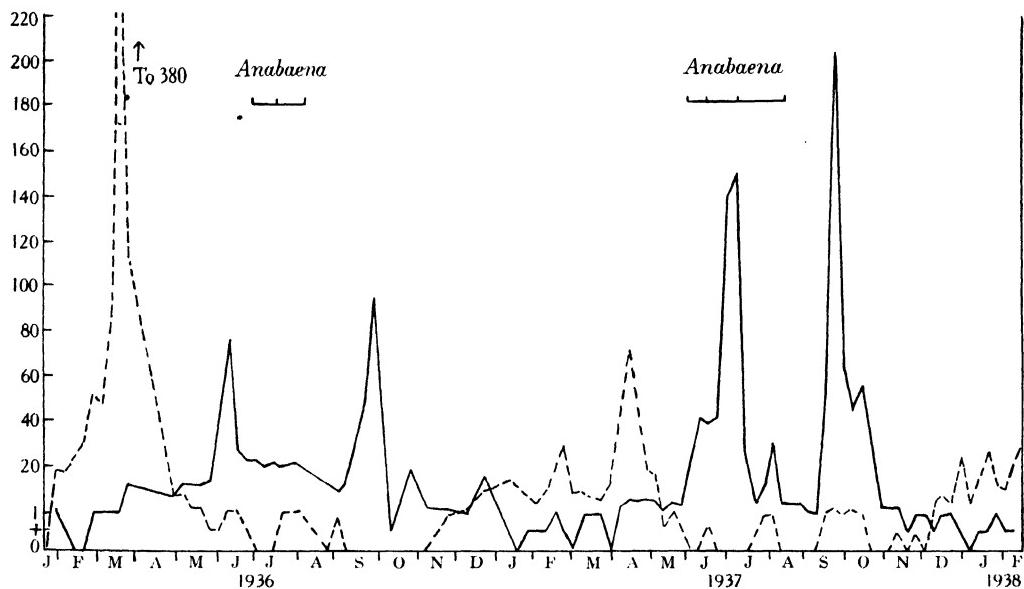


Fig. 3. Upper Pen Pond, area E, upper littoral. Seasonal variation of planktonic and bottom-living algae. Summer-autumn, mainly bottom-living flagellates (continuous line): *Chlamydomonas* spp., *Cryptomonas* B, C, *Chromulina ferrea*, *Chromulina* spp., *Mallomonas limnicola*, *M. radiata*, *Ochromallomonas pelophila*, *Sphaeromantis ochracea*, Euglenineae. Winter, planktonic flagellates (interrupted line): *Chrysococcus rufescens*, *Kephryion littorale*, *Mallomonas akromonas*, *Dinobryon* spp., 'Zoospores' (Chlorophyceae), *Cryptomonas* C. (small form); (horizontal line) *Anabaena flos-aquae*, lesser amounts of *A. affinis* (period of abundance).

During the earlier part of this phase, rain and wind disturb the deposit, but this does not result in admixture with the adjacent lower littoral region, owing to the protective *Juncus* belt. The pH, generally 6.5-6.8, rises to about 7.5 at certain times, but never reaches the very alkaline state typical of the lower littoral area. Indeed, the demarcation between upper and lower littoral regions is not only indicated by the flora, the type of bottom deposit and the boundary constituted by the *Juncus* bed, but also by the sudden change in the pH value of the water. On 22 July 1937, the pH varied, within 3 ft., from 6.9 at the outer edge of the upper littoral to 8.9 just outside the *Juncus* zone and 9.0-9.2, 30 cm. beyond it.

During the second phase the plankton organisms of the preceding phase are absent except for a few specimens of *Chrysococcus rufescens*. The bottom-living flora and also to some extent that of the overlying shallow water become very rich in flagellates (Fig. 3).

Species of *Chlamydomonas*, *Cryptomonas* and *Mallomonas*, *Ochromallomonas pelophila*, *Sphaleromantis ochracea* and *Euglenineae* (especially species of *Trachelomonas*) are among the commonest. *Chromulina ferrea* n.sp. is abundant, at times forming a brown film on the surface. Diatoms are also present, notably *Nitzschia palea*, *Pinnularia viridis*, *P. major* and *Stauroneis anceps*, but they are not so numerous as on the exposed mud later in the season.

Temperature does not appear to be a factor directly determining the occurrence of this flora, though it has an indirect action in accelerating the rate of decomposition of the deposit. In 1937 a small puddle, segregated from the rest of the area, retained the rich flagellate flora (esp. *Euglenineae* and species of *Oscillatoria*) up to the end of November, despite the low temperature with some ice formation.

The part of the margin of area E exposed from mid-June to September in 1937 was dominated by creeping algae. Motile forms, except for minute species of *Chlamydomonas*, were represented only by resting stages; samples kept under water in the laboratory for a day or two, however, produced the flagellates typical of the submerged period. *Euglena mutabilis*, a species usually lacking a flagellum, occurs in some quantity when the mud is strongly acid. The dominant algae on the exposed, water-saturated mud are species of *Oscillatoria* (*O. tenuis*, *O. splendida*) and *Anabaena* (*A. oscillarioides*?), pennate diatoms belonging to the Raphidiodeae (*Nitzschia palea*, *Stauroneis anceps*, *Pinnularia* spp., etc.) and the small species of *Chlamydomonas* just referred to. The tiny puddles left in the exposed area have a rich flora including organisms characteristic both of the submerged regions and of the exposed mud. The whole flora is like that in the similar habitat of the Upper Pond (pp. 264-265).

(b) The lower littoral beyond the *Juncus* zone possesses a wholly different bottom flora. The plankton, though identical in the first phase (winter-spring), is very poor, and the flagellates of the lower littoral (second phase) are only represented by species of *Cryptomonas*. There was a brief water-bloom due to *Anabaena flos-aquae*.

The difference in the bottom flora (Table 1) may be connected with the different type of deposit present. This consists of a thin layer of black to brown ooze composed of silt and the excrement of small aquatic animals, overlying sand; numerous dead diatom cells are present. The organic content is low (2·6-4·3 %) and the deposit is calcium deficient, but does not give a strong reaction. The surface is black during winter; in early spring the abundant diatoms colour it a dull brown, and in summer it is reddish brown due to the ferric oxide present. A remarkable feature of this zone is the extreme alkalinity of the water during summer, when the pH remains at 9·0-9·2 for long periods; in winter it is somewhat acid (6·5 av.).

The bottom flora is always rich in pennate diatoms (largely Raphidiodeae), but the species are different from those of the upper littoral and are very numerous. They include many of the larger *Surirellas* and *Cymatopleuras*, as well as *Nitzschia sigmaoidea*, *N. Tryblionella*, *N. flexa*, *Navicula cuspidata*, *Stauroneis acuta*, etc. (Table 1). The dominant form is *Fragilaria construens*, which is always abundant. The diatoms reach their maximum in January and February. In July and August *Spirogyra nitida* covers large stretches of the bottom, while species of *Scenedesmus* are common and *Pediastrum boryanum* is usually present, though only in small numbers. Myxophyceae are only represented by *Microcystis parasitica* and *Aphanothecete stagnina*. The presence of *Fragilaria construens* and species of *Scenedesmus* in the upper littoral is due to contamination from this area.

All the algae found commonly on the bottom deposit in this zone, with the exception of *Fragilaria construens* and species of *Scenedesmus*, possess some means of motility enabling them to regain the surface if buried. Owing to the greater depth (20–60 cm.) and situation of this zone, displacement of the fine particles of the deposit is much less frequent than in the upper littoral, though the strong winter gales sometimes cause furrowing of the deposit due to wave action.

Monthly observations of the epiphytic flora on the macrophytes in and around area E show that it does not include any of the characteristic bottom forms nor does it constitute a breeding ground for them. During, and especially towards the end of the period of abundance of certain epiphytes (*Synedra pulchella*, *S. ulna*, *S. amphicephala*, *Diatoma vulgare*, *Gomphonema parvulum*, etc.), numerous cells fall on to the bottom. ‘Entangling’ growths of diverse filamentous Chlorophyceae occurring among the epiphytes are, moreover, often swept into this area.

(ii) *Area F* occupies a shallow bay lacking any protective belt of macrophytes. The sandy bottom is admixed with clay, resulting from the erosion of the banks, which leads to the formation of a definite ‘beach’. Owing to the exposed position, the area is subject to severe wave action which prevents any accumulation of organic material so that the percentage of the latter is always very low (0·27–0·54).

The plankton, both in summer and winter, is similar to that of the lower littoral region of area E, while *Fragilaria construens* dominates the bottom flora throughout the year. This alga is, no doubt, recruited from the adjacent lower littoral, where it is again very abundant. The upper littoral flora typical of area E in summer and autumn is absent, though the characteristic species are sometimes found, probably introduced from the areas on either side which resemble area E. The lower littoral region of area F was only occasionally examined, but its flora proved to be almost identical with that of area E.

Other parts of the upper and lower littoral regions of this pond were examined from time to time. Whenever the area was subject to the same physical and chemical factors as occur in areas E and F respectively, the upper littoral flora was of the same type, though the species of flagellates varied somewhat. The lower littoral region showed remarkable uniformity throughout. The Lower Pen Pond is similar to the Upper one in the nature of the substratum, the types of bottom deposit and the drainage area surrounding it; moreover, it receives the bulk of its water from the Upper Pond.

#### (iv) *The Upper Pen Pond*

The margin of the Upper Pen Pond, the largest of the ponds, is largely colonized by *Juncus communis* and *J. articulatus*, accompanied by *Myriophyllum verticillatum* and a species of *Nitella* in the deeper waters. Over the greater part the depth does not exceed 2 m. For a long or shorter period in the summer the flow from the drains and streams passing into the pond ceases, and it becomes stagnant. Two areas, possessing markedly different substrata, were examined. Area C comprises upper and lower littoral zones (the latter studied after January 1937), while area D is close at hand. The upper littoral region of area C is rich in decomposing vegetable matter, while area D is more exposed and has a purely sandy substratum.

(a) The upper littoral of area C lies between the edge of the pond and a narrow bank of *Juncus communis* some 4 m. towards the open water. The latter affords some shelter, though owing to its limited extent and the exposed, shallow nature of area C, not so

effectively as in area E in the Lower Pond. The bottom deposit is rich in organic matter (10.6–27.7 %), which is largely derived from leaves of trees, although a considerable amount of other detritus is washed in during the autumn. The deposit is shallow and little methane is produced; it is markedly calcium deficient.

The flora resembles that of the similar area E in the Lower Pond, though the summer flagellate communities are not so well developed. The autumn-spring phase (October or November to June) is much the same. In the autumn the rise in water-level and the dying down of the sheltering *Juncus* are accompanied by the addition of new leaves. Since area C is more exposed than E, the rainfall and strong winds cause frequent disturbance of the deposit. The bottom flora in autumn and winter is, therefore, very poor and with the low-temperature decomposition of the black deposit proceeds very slowly.

There is a rich plankton resembling that of the lower littoral and of the Lower Pen Pond. *Chrysococcus rufescens* var. *tripora* is dominant and occasionally tinges the water a faint brown. Species of *Dinobryon*, *Mallomonas*, *Cryptomonas* and *Kephyrion littorale*, as well as Chlorophycean zoospores, also occur in this largely nannoplankton community. In the spring *Ankistrodesmus falcatus* and other Chlorococcales accompanied by *Asterionella formosa* and *Cyclotella comta* are present in small numbers. The bottom flora (cf. above) is very poor; it includes a few individuals of *Pinnularia maior*, *P. viridis* and *Stauroneis anceps*.

From the end of May to late September (1936) or late October (1937) a different flora occurs. The flagellate phase was poorly represented in the wet summer of 1936 but better developed in 1937, in which almost the whole area became exposed early in the summer. The deposit undergoes the same changes as in area E (p. 261). The marked swelling and the rapidity with which it becomes exposed renders the underwater flora less prominent than in area E, Lower Pen Pond. While the pH during the first phase is always acid (6.3–6.9) it tends to be higher, the water sometimes reaching a neutral or slightly alkaline reaction in the second.

During this second phase the plankton organisms of the previous one are represented only by occasional individuals of *Chrysococcus rufescens* var. *tripora*. The plankton is generally poor, although there are short periods of water-bloom due to *Microcystis aeruginosa* and *Anabaena flos-aquae*. It differs from that of the Lower Pond in the presence of *Urogljenopsis americana* during November and early December.

The exposed deposit in 1937 was occupied by a flora similar in all respects to that of area E in the Lower Pond. It was dominated by creeping algae, while motile forms were represented only by minute species of *Chlamydomonas*. Samples covered with water in the laboratory again produced the flagellates of the submerged regions. The small puddles remaining in the exposed mud contain not only the creeping algae typical of the exposed mud, but also a rich flagellate flora more like that of area E (Lower Pond) than that of the submerged zone of the upper littoral of area C. Euglenineae, *Chromulina ferrea* n.sp., species of *Mallomonas* and of *Cryptomonas*, all occurred abundantly, and in the early stages of exposure of the mud were also found to some extent upon it. It is clear that the poorer representation of the flagellate community in area C, as compared with area E, in 1937 at least, is due to rapid exposure so that there was insufficient time for the full flora to develop.

The flora of the exposed mud was dominated by *Oscillatoria* (largely *O. tenuis*, *O. splendida*), *Anabaena* (*A. oscillarioides*?), species of *Chlamydomonas* and diatoms (*Nitzschia*

*palea*, *Stauroneis anceps*, species of *Pinnularia*, etc.). *Euglena mutabilis* occurred especially at the end of the period of exposure when the pH fell to approximately 5·0.

(b) The Lower Littoral area lying beyond the *Juncus* zone differs altogether in its bottom deposit and flora. The former consists of a thin layer of fine grey ooze overlying sand, and has an organic content of 1·3–3·3 % (average 2·4 %), even lower than that of the deposit in the lower littoral area of E (average 3·3 %). It undergoes no visible alteration during the year and contains practically no remains of leaves; laboratory observations show that it does not swell like the upper littoral deposit (p. 272). Only very rarely did a calcium-deficiency test produce a positive result. The particles of the ooze consist largely of fine silt, diatom frustules and coprogenous matter.

In the autumn-spring phase, the plankton above this deposit is exactly like that of the upper littoral. In November and early December (1937) it was dominated by abundant *Uroglénopsis americana*, while from January to May *Chrysococcus rufescens*, accompanied by other planktonic Chrysophyceae, was the most abundant alga. In the second phase (summer-autumn) the plankton was poor except for occasional water-bloom due to *Microcystis aeruginosa* and *Anabaena flos-aquae*. The pH of the water is 6·3–7·0 during the first phase, but more alkaline during the second (7·0–7·5), although the high degree of alkalinity characteristic of the lower littoral area of the Lower Pond never occurs.

The bottom-living flora is always rich in pennate diatoms (Rhaphidiodeae), the most characteristic being *Nitzschia dubia*, *N. acuta*, *N. palea*, *Navicula rhyncocephala*, *Caloneis silicula*, *Neidium producta* and species of *Surirella*, while, as in area A, *Fragilaria construens* is the dominant species. Species of *Scenedesmus* (especially *C. longus*) are also common, while *Pediastrum boryanum* is generally present in small numbers. In spite of the general similarity with area E, differences in specific constitution are shown by the presence of such algae as *Nitzschia dubia*, *Caloneis silicula*, and *Surirella spiralis* and the greater rarity of such species as *Nitzschia recta*, *N. flexa*, *N. sigmoidea*, *N. Tryblionella*, *Navicula cuspidata*, *Surirella Capronii*, *Cymatopleura elliptica*, *C. solea*, and *Gyrosigma acuminatum*. The lower littoral region of area C, moreover, possesses two characteristic Myxophyceae, *Holopedium geminatum* and *Coelosphaerium limnicolum* n.sp., which were entirely absent from the corresponding region of E, though the former occurred elsewhere in the littoral region of the Lower Pond. These two algae were rarely obtained in measurable amount in the suction samples, but were at times very evident in the ‘one-day’ samples; the colonies, though not numerically abundant, are so large (Lund, in the press) as to be individually equivalent to a number of the smaller algae. *Aphanocapsa stagnina* is also sometimes present on the bottom deposit, as well as *Tolypothrix tenuis* and a species of *Mougeotia*; *Spirogyra nitida* is completely absent.

As in the upper littoral region and in the Lower Pond, the great majority of the algae living on or near the bottom deposit possess some means of motility and so can regain the surface after burial (see p. 275).

Area D consists of a bay with a gently sloping shore and, except for the absence of a clay bank, exactly parallels area F in the Lower Pond (organic content of deposit 0·46–0·55 %). It is very barren owing to frequent and violent disturbance, and the description of area F applies equally well to it.

The most important features emerging from the study of these ponds are:

(1) The similarity of the Clay Pit's flora, in nature and in laboratory cultures (p. 267),

with the floras of the upper littoral area (C and E) of the Pen Ponds (especially in summer and autumn).

The qualitative, but not quantitative, restriction of the plankton and bottom flora of the above areas and the predominance of flagellates, which are considered to be connected with the richness of the deposits in organic matter and the stagnant conditions. The flagellate maxima occur, in areas C and E, in summer and autumn when the ponds are stagnant and in autumn and early winter in the Clay Pit which is always stagnant.

The difference, in these areas, between the flora of the exposed mud and that at the surface of the deposit in the open water.

(2) The importance of wave action in determining the presence or absence of a deposit rich in vegetable matter (e.g. areas C and E compared with D and F) and, together with rainfall, in affecting the seasonal variation of the upper littoral areas C and E.

(3) The marked difference in the deposits and in the floras associated with them in the upper and lower littoral zones of the Pen Ponds. The deposits of the latter zones and that of area B (Leg-of-Mutton Pond) are only occasionally disturbed and, in both, the non-motile *Scenedesmus* spp. (especially *S. longus*) and *Fragilaria construens* are frequent or very abundant.

(4) The marked difference between the flora of the Leg-of-Mutton Pond (especially area B) and those of the Clay Pit and Pen Ponds (especially the upper littoral areas C and E) due probably to the lesser organic content of the deposit and the high acidity of the water during a large part of the year. The deposit of area A is more like the latter areas than that in area B, and the flora shows a correspondingly greater similarity.

The absence of phytoplankton in the Leg-of-Mutton Pond and the massing of *Scourfieldia complanata* and *Chromulina ovalis* near the bottom in spite of their positive phototaxis, together with the great similarity of the flora in the two areas throughout the period of high acidity.

The absence of the Euglenineae-*Chlamydomonas*-*Cryptomonas*-*Oscillatoria* phase typical of area A during the less acid phase from area B where, also, *Scenedesmus longus* and *Fragilaria construens* are always much more abundant, may be connected with the thinner and less organic deposit in the latter area.

(5) The motility of the great majority of the bottom-living forms, enabling them to recover from the effects of disturbance. These algae are not recruited from the plankton or epiphytes, but form a distinct community.

#### IV. LABORATORY OBSERVATIONS

##### (1) *Cultures in distilled water*

Numerous cultures were made with the object of discovering what type of flora could be produced from samples of the various bottom deposits when not enriched in any way. Owing to the varying nature of the deposits it was impossible to procure altogether equivalent volumes at different times of the year. The samples were placed in crystallizing dishes with about 200 ml. or pint bottles with about 400 ml. of glass-distilled water and examined fortnightly or monthly. The cultures were well illuminated but screened from direct sunshine. Only a few of the detailed results are given here (Tables 2-5). The sequence followed is the same as in § III.

*(a) The Clay Pit*

All the samples of bottom deposit from the *Clay Pit* consisted of clay, oak leaves and twigs. Some leaves were always undecomposed, since there was never complete disintegration even in the surface layers. The disturbance resulting on collection led to disappearance of the brown surface layer (p. 249), the ferric salts being reduced to the ferrous state. In summer the surface layer often became brown again within 24 hr. in the cultures, but in autumn and winter more than a month might elapse before it was reformed. It took longer to appear in the bottles than in the dishes, no doubt owing to less easy access of oxygen.

The stages in the decomposition of the deposit and the accompanying changes in the algal flora are best shown in autumn and winter cultures to which the following description applies (Table 2). Visible decomposition commences after a month or so. The surface layers gradually become brown and the contained leaves break down to form a mud rich in humus, a process accompanied by considerable swelling so that the deposit acquires four to five times its original volume. The production of plentiful methane in the lower layers also tends to raise the deposit, and parts of it are sometimes lifted up to the surface with the bubbles. The deposit now fills the dishes so that no supernatant water remains, although this is not so in the bottles owing to their greater depth. The whole process, moreover, is slower in the latter. Ultimately, as production of methane ceases, the deposit shrinks somewhat, but it never returns to its original volume. A completely disintegrated surface layer does not always occur, one or more leaves often remaining complete. This suggests that the water can only support the decomposition of a certain amount of organic matter and that after a time it reaches a state of 'saturation'.

In the bottles (Table 2) the flora is first dominated by colourless flagellates (*Chilomonas paramaecium*, *Euglenineae*), motile bacteria (including usually the iron bacterium, *Ochrobium tecta*), Protozoa (*Diffugia*, *Amoeba*), and ciliates, while a few pigmented Euglenineae are also present. *Ochrobium tecta*, which is common in the lower layers of the pond water, sometimes reappears at a later stage. Sulphur bacteria are only rarely present. During the early stages of decomposition of the surface layers one finds Euglenineae (especially species of *Trachelomonas*) and *Cryptomonas*, together with species of *Pinnularia*. The colourless organisms decrease in number, and bacteria, though still abundant, consist largely of non-motile forms.

In the third stage, when the swelling of the deposit reaches its maximum, there is a decrease in flagellates and an increase in diatoms (*Pinnularia gibba*, *P. maior*, *P. microstauron*, *P. viridis*, *Stauroneis anceps* f. *gracilis*, *S. phoenicentron*, *Nitzschia palea*) and various filamentous algae (*Chaetophora elegans*, *Microspora stagnorum*, *Tribonema affine*, etc.); *Ophiocytium arbuscula* also becomes frequent. In still later stages *Anabaena oscillarioides* becomes dominant and certain species of *Closterium* (viz. *C. Malvinacearum*, *C. striolatum*, *C. venus*) are characteristic, though rarely frequent. A number of epiphytes that are common in the pond are now found abundantly, especially *Eunotia arcus*, *E. linearis*, *Achnanthes minutissima* and the filamentous algae mentioned above. The algae occurring in these diverse stages are present in the *Clay Pit* itself or are found on the wet mud around the edges in summer (Table 1).

In the dishes the first two stages are less prominent and last for a shorter length of time, differences which can be correlated with the faster decomposition and progressive diminution of the supernatant water owing to the swelling of the deposit. Diatoms are abundant,

## *Marginal algae of ponds*

Table 2. More important algae, etc., in culture of deposit from the Clay Pit (bottle culture) (see text, p. 266). In this and succeeding tables the genera are grouped in the order followed by Fritsch & West (1927); the species of the genera enumerated collectively are the same as occur in nature

Months	Motile bacteria, Protozoa, ciliates	vii	viii
i	Ochromium tecta	r.	.
ii	Ochromium tecta	a.	.
iii	Chromatium sp.	a.	v.r.
iv	Chlamydomonas parameciuum	a.	.
v	Chlamydomonas spp.	o.	.
vi	Microsphaera stagnorum	r.	.
vii	Chaetophora elegans	o.	.
viii	Closterium venus	r.	.
ix	C. striolatum	v.r.	.
x	C. Malvinacearum	.	.
xi	Ophiocytium arbuscula	.	.
ii	Tribonema affine	.	.
iii	Pinnularia gibba	.	.
iv	P. mesolepta	v.r.	.
v	P. major	.	.
vi	P. viridis	o.	.
vii	Sphaureis phoenicentron	r.	.
viii	Nitzschia palea	v.r.	.
ix	Cryptomonas spp.	o.	.
x	Euglena intermedia	.	.
xi	E. spirogyra	.	.
ii	Euglena spp.	v.r.	.
iii	Phacus pleuronectes	.	.
iv	P. pyrum	.	.
v	Phaeus spp.	r.	.
vi	Trachelomonas hispida	v.r.	.
vii	T. varians	a.	.
viii	Anabaena oscillarioides	f.	.

some filamentous algae occur, and species of *Closterium* are generally present. The flora in the dishes resembles that of the exposed mud in nature, except for the presence of filamentous algae. The occurrence of the latter is rendered possible by the saturation of the air above the mud surface in the covered dishes. An alga, almost invariably abundant in the later stages of these cultures, is *Chromulina aerophila*, which, however, has never been observed in the Clay Pit.

In both sets of cultures, as the process of decomposition continues, the water becomes increasingly opalescent and brown owing to the presence of large amounts of colloidal ferric oxide. Cultures set up in spring and summer show similar but less marked changes.

(b) *The Leg-of-Mutton Pond*

(i) In area A of the Leg-of-Mutton pond the deposit consists of silt and the remnants of *Juncus*, *Equisetum* and bracken, and when brought into the laboratory rapidly becomes rusty brown. Apart from this, however, no visible change takes place and no such sequence as has been described for the Clay Pit occurs. The dish and bottle cultures show no clear differences. The presence of similar plant remains to those in area B results in the occurrence of many forms common in that area in nature, as well as in cultures made from its deposits. These include *Scenedesmus longus* and other species of the genus, *Desmatractum bipyramidatum* and *Fragilaria construens*, all of which were found, although in lesser numbers, in area A in nature.

The pH of the samples is generally 6.0–7.0, but some cultures become very acid with a pH below 5.0, such as is found in the pond itself during winter and early summer. Chrysophyceae are very common in all the cultures, while Euglenineae are infrequent in spite of the stagnant conditions. *Chrysamoeba radians*, *Dinobryon sertularia*, *Hyalobryon ramosum* and *Lagynion Scherffelii* are the most important Chrysophyceae. *Cryptomonas* is only an occasional form, but a palmelloid member of Cryptophyceae was very abundant in some cultures. Peridineae are frequently present in small numbers, and in a few cultures *Glenodinium uliginosum* was very common. Species of *Oscillatoria* are often present in quantity, while *Cylindrospermum alatosporum*, though not observed in nature, was abundant in three cultures. Species of *Closterium* occur in small numbers, while *Micrassterias rotata* is sometimes frequent. *Mougeotia viridis*, *Hormidium subtile* and *Microthamnion Kuetzingianum* are the commonest of the filamentous green algae. It is noteworthy that, except for the *Cylindrospermum*, all the forms that are common or abundant in the laboratory cultures are typical of the area and of the pond as a whole, in spite of the absence of any enrichment. They include bottom-living (*Scenedesmus longus*, species of *Closterium*, *Oscillatoria limosa*, *O. splendida*, *O. tenuis*, *Cryptomonas*, Euglenineae), epiphytic (*Hormidium subtile*, *Microthamnion Kuetzingianum*, *Bulbochaete subintermedia*, *Mougeotia viridis*, *Chrysamoeba radians*, *Lagynion Scherffelii*) and planktonic algae (*Chrysococcus rufescens*, *Dinobryon sertularia*, Peridineae).

(ii) The deposit from area B (see p. 252) undergoes very little visible change in the laboratory. The fragments of *Juncus* and bracken<sup>1</sup> decompose extremely slowly, and the deposit never becomes brown at the surface, nor is there any swelling or methane production. The water was highly acid (pH 5.5–4.0) for most of the period during which any one culture was under observation. The high acidity of the supernatant water in these cultures is of interest, since in the pond the very acid phase spreads from the inlet near

<sup>1</sup> A piece of bracken frond was not completely disintegrated after two years in the laboratory.

area A subsequent to the change in pH of the inflowing water. In the summer, on the other hand, when there is little or no inflowing water, the pH rises. The very high acidity in the cultures suggests that acidity in the pond depends not only on the influence of the inflowing water.

As in area A, the algae appearing in the cultures, with rare exceptions, are those typical of the area in nature. Not only the bottom-living forms (*Scenedesmus*, *Desmatostratum*, *Fragilaria*, *Scourfieldia*), but also many of the common epiphytic and entangling algae (*Hormidium*, *Mougeotia viridis*, *Dicranochaete*, *Chrysamoeba*) occur. Plankton forms are not common, and it will be recalled that they are entirely absent during the acid phase in the pond. In cultures which do not develop so high a degree of acidity, or during less acid phases, Peridineae, *Chrysococcus* and *Dinobryon* may be present. The rarity of *Chromulina ovalis* is remarkable.

### (c) *The Pen Ponds*

(1) Cultures from the deposits of the upper littoral areas (C and E) of the Pen Ponds show close similarity. Samples gathered between late autumn and spring are rich in undecomposed leaves and other vegetable detritus and are black throughout, while, as summer progresses, the amount of non-disintegrated matter becomes less and less until the deposit consists merely of a fine mud with a brown surface. Removal to the laboratory always results in a temporary loss of the brown surface owing to the strong reducing action of the lower layers. The more decomposed the deposit is, the sooner does the brown colour reappear in the cultures.

In the cultures undertaken from late autumn to spring the successive changes in the deposit and the accompanying change in the algal flora can be followed (Table 4), while cultures started in summer only show certain phases of the algal flora.

As long as the deposits are black throughout and reductive (Comber-Misra test) the dominant organisms are motile bacteria, ciliates and Protozoa (*Diffugia*, *Arcella*, *Amoeba*) and diverse colourless algae. *Chilomonas paramaecium* is almost always abundant, while colourless Euglenineae (especially *Menoidium*), *Polytoma*, *Monas* and other Protomastigineae are frequently present, sometimes in abundance. This phase generally lasted from 3 to 5 weeks, but may persist longer (up to 2 months). The cultures have no disagreeable odour, but they are clearly putrid, since large quantities of methane are produced, while bacterial slimes often cover the surface.

At the close of this phase the flora in the bottles becomes replaced by pigmented flagellates (Table 4) while the abundant bacteria are now nearly all non-motile. The dominant forms in this phase, lasting from 11 weeks to 4 months, are species of *Cryptomonas*, *Euglena*, *Lepocinclis*, *Phacus*, *Trachelomonas* and *Chlamydomonas*: the two latter are often very abundant. Certain characteristic pennate diatoms become very plentiful in later stages; the commonest are *Nitzschia palea*, *Pinnularia maior*, *P. viridis*, *Stauroneis anceps*, *S. phoenicentron* and *Navicula cryptocephala*. As the vegetable matter breaks down, more and more of the deposit becomes brown with ferric oxide, while the water shows opalescence due to colloidal ferric hydroxide or oxide. Anaerobic decomposition is less, as shown by the reduced amount of methane produced. The sample swells to as much as four or five times the original volume. The pH remains between 6.0 and 7.0 (usually 6.5).

The third stage, occurring from about the fourth month onwards, is realized when the

Table 3. Cultures of sample of deposit from the Leg-of-Mutton pond, area A  
(bottle culture, see p. 268 for method of compilation)

Months	...	iii	iv	v	vi	vii	viii
	<i>Chlamydomonas</i> sp.	v.r.	.	.	.	.	.
	<i>Scenedesmus longus</i> et spp.	v.r.	r.	r.	r.	r.	r.
	<i>Bulbochaete subintermedia</i>	.	.	.	r.	r.	r.
	<i>Oedogonium</i> sp.	.	.	r.	r.	r.	r.
	<i>Mougeotia viride</i>	.	.	r.	r.	r.	r.
	<i>Chromulina</i> sp.	.	.	.	.	r.	r.
	<i>Hydrobryon sertularia</i>	.	.	r.	r.	r.	r.
	<i>Cryptomonas</i> B, C	.	.	a.	r.	r.	r.
	<i>Glenodinium uliginosum</i>	.	.	f.	v.r.	v.r.	r.
	<i>Gymnodinium</i> sp.	.	.	r.	r.	r.	r.
	<i>Peridinium</i> spp.	.	.	.	r.	r.	r.
	<i>Trachelomonas</i> spp.	.	v.r.	r.	r.	r.	r.
	<i>Cyindrospermum alatosporum</i>	.	v.r.	r.	r.	a.	a.
	<i>Oscillatoria splendida</i>	.	.	.	.	o.	o.

Table 4. Culture of sample of bottom deposit from the upper littoral of the Lower Pen Pond (area E) placed in bottle and covered with 400 ml. of glass-distilled water (Pyrex). For method of compilation see Table 2, p. 268

swelling of the deposit and methane production have ceased and the great part of the deposit is brown (i.e. oxidized). The pH remains slightly acid. Flagellates, except for a species of *Chromulina*, have become rare, while diatoms and blue-green algae (*Oscillatoria splendida*, *O. tenuis*, *Cylindrospermum alatosporum* or *Anabaena oscillarioides*) are abundant. Other algae often present are *Ophiocytium arbuscula*, *Tribonema affine* and certain filamentous Chlorophyceae (*Microspora stagnina*, *Oedogonium* spp., *Mougeotia* sp.). *Closterium Leibleinii* and *C. striolatum*, though not common, are very characteristic.

In the dishes the swelling deposit leaves only a surface film of water, so that there is only a scanty development of pigmented flagellates. On the other hand, the same diatoms and species of *Oscillatoria* are abundant, accompanied by the *Closteria*. Certain epiphytes occur on the surface of the deposit, notably *Achnanthes minutissima*, *Gomphonema parvulum* and *Eunotia arcus*. In later stages, when owing to shrinkage of the deposit free water is again present, filamentous algae are sometimes found. Certain cultures which became very acid in later stages contained *Chromulina aerophila* n.sp. (Lund, in the press) and *Hormidium subtile*.

Table 5. *Algae present in culture of deposit from the lower littoral of the Lower Pen Pond (dish cultures, see p. 268 for method of compilation)*

Months	...	vi	vi	vii	vii	viii	ix	ix	x	xi	xii
pH	...	7.3	7.1	6.8	5.7	4.6	4.0	4.2	4.2	4.2	3.8
<i>Scourfieldia complanata</i>	.	.	.	.	.	.	.	.	.	a.	a.
<i>Stigeocolonium tenue</i>	r.	f.	r.	.	.	.	.	.	.	.	.
<i>Spirogyra nitida</i>	.	v.r.	f.	a.	f.	.	.	.	.	.	.
<i>Fragilaria construens</i>	o.	f.	f.	o.	r.	.	v.r.	.	.	.	.
<i>Synedra pulchella</i>	r.	f.	o.	o.	.	.	.	.	.	.	.
<i>Pinnularia viridis</i>	.	.	.	.	.	v.r.	v.r.	r.	o.	o.	.
<i>Gomphonema parvulum</i>	f.	.	.	.	.	.	.	.	.	.	.
<i>Nitzschia acicularis</i>	o.	f.	.	.	.	.	.	.	.	.	.
<i>Suirella robusta</i>	.	r.	r.	r.	f.	r.	r.	.	.	.	.
<i>Cryptomonas</i> spp.	r.	o.	f.	f.	o.	r.	f.	a.	a.	a.	o.

(2) In the lower littoral areas the deposit from area E (Lower pond) is black, while that from area C (Upper pond) is usually greyish (sometimes black). In cultures the surface of both deposits becomes brown after 2 months or more and the depth of the brown layer increases with time. There is no other visible change, neither swelling nor methane production. The pH is at first more or less alkaline (to 8.5), but after a period of 2-3 months becomes highly acid; almost always below 5.0 and sometimes as low as 3.8 (cf. area A, Leg-of-Mutton Pond). The water of area C is generally almost neutral or definitely alkaline (pH to 7.5), while that of area E is very strongly alkaline during summer and autumn (pH to 9.4); in neither area does the pH ever fall to values comparable to those observed in the cultures.

At first the flora in the cultures comprises numerous species (to about 60), for the most part those characteristic of the respective areas in nature and including planktonic, epiphytic and bottom-living forms. The planktonic forms belong chiefly to Chlorococcales and Myxophyceae (*Anabaena affine*), though *Nitzschia acicularis* is often important (Table 5). When the cultures become highly acid the number of species drops to ten or less, *Scourfieldia complanata*, *Hormidium subtile*, *Cryptomonas* and *Pinnularia viridis* being abundant. The first two are absent from these areas in nature though typical of the acid Leg-of-Mutton Pond, in acid cultures of which the *Cryptomonas* is also found. *Pinnularia viridis* may occur in acid cultures from the upper littoral of the Pen Ponds.

The dish cultures contrast with the bottle cultures in the frequent abundance of *Chromulina aerophila*.

(ii) *Cultures with special additions*

Certain cultures were made with various additions (Benecke solution, single salts, bracken litter, oak leaves, *Juncus* shoots, etc.). In several of them, especially those enriched with 0·05 % Benecke solution, very acid conditions were realized ( $pH$  4·0–5·0) and forms appeared which are to be regarded as acid-loving. Among the most important were: *Scourfieldia complanata*, *Characium Pringsheimii*, *Hormidium subtile*, *Microthamnion Kuetzingianum*, *Mougeotia viridis*, *Chromulina aerophila* n.sp. forma B, *Cryptomonas* sp., *Euglena mutabilis*.

Another series of cultures was kept constantly aerated. Those made up with deposits from the Leg-of-Mutton Pond and the upper littoral regions of the Pen Ponds (areas C and E) showed great rarity or absence of flagellates, except for *Cryptomonas* sp., although they were abundant in the non-aerated cultures set up at the same time. The aerated cultures from the Clay Pit and Leg-of-Mutton Pond bore but a very poor flora, while those with deposits from the Pen Ponds were dominated by filamentous and epiphytic algae.

The important features of these cultures are:

(1) The bottom deposit contains the substances necessary for the growth of the great majority of the algae common in the Clay Pit and the upper littoral areas of the Pen Ponds (areas C and E), especially from late spring to autumn. Notable absentees are certain plankton algae (*Synura uvelia* and *Mallomonas acaroides* in the Clay Pit, planktonic Chrysophyceae and Myxophyceae in the Pen Ponds) and the bottom-living *Spirogyra nitida* in the Clay Pit. The numerous flagellates of these areas, apart from the absentees mentioned above, though occurring throughout the water, are probably mud-inhabiting forms, their occurrence throughout the water being ascribed to the stagnant conditions in these areas, the whole of the water, which is shallow, being saturated with the products of decomposition of the bottom deposit. These cultures show an analogous series of changes as in the purification of sewage (Kolwitz & Marsson, 1908), although the starting point is altogether different. Even in cultures maintained for two years, however, no further advance occurred, while in nature the process is arrested each autumn by the influx of fresh dead vegetable matter. The first stage, with colourless saprophytes dominant, has not been seen in nature apart from indications in the upper littoral regions of the Pen Ponds, and may be ascribed to the more marked stagnation of the water in the laboratory resulting from the relatively large proportion of mud to water in the cultures. Pennate diatoms, *Anabaena oscillarioides* and *Oscillatoria* spp., which play a considerable part in the cultures, are rarely frequent on the pond bottom (see p. 256, Table 1), but occur in the small puddles in the mud at the pond margins. When supernatant water is absent (dish cultures) the flora closely resembles that found on the wet mud in nature. The very acid stage dominated by *Chromulina aerophila* was never realized in nature.

(2) The cultures from the Leg-of-Mutton Pond again include nearly all the typical algae of the pond, showing that the deposit alone can support a natural flora. This flora, however, is very different from that of the Clay Pit and upper littoral areas (C and E) of the Pen Ponds which, as in the actual pond, can be correlated with the different structure of the deposit and often highly acid conditions.

(3) In the cultures from the lower littoral areas of the Pen Ponds (C and E) the changes

in the flora contrast with the very constant character of the bottom flora in nature. None of the algae typical of the areas become frequent, their occurrence in early stages being no doubt due to their presence in the sample. In contrast to cultures of deposits from the other ponds, these deposits do not possess the capacity to produce floras similar to those occurring in nature. It appears possible, therefore, that the production of the natural flora on the deeper sediments and *pH* in the supernatant water is dependent on the continuous addition of suitable substances (e.g. silt and plankton debris).

## V. GENERAL CONSIDERATIONS

### (1) Temperature

This does not appear to be important in relation to the growth of the marginal bottom-living forms. The absence of the flagellate-diatom communities in the upper littoral areas during winter is probably not to be ascribed to the temperature, but to the presence of fresh leaves and other vegetable detritus, the high-water level and the frequent wind action. The flagellate community in area A (Leg-of-Mutton Pond) continued into December, and the greatest abundance of Euglenineae in the Clay Pit was realized in October and November. In the upper littoral of the Pen Ponds, on the other hand, it occurred when temperatures were at their highest.

The planktonic Chrysophyceae are largely winter forms, while the bottom-living species (*Ochromallomonas*, *Mallomonas limnicola*, etc.) are summer-autumn forms.

### (2) Hydrogen-ion concentration

The *pH* values vary greatly, even in one and the same pond at different times of year (e.g. littoral areas of the Lower Pen Pond).

During the exceptionally acid phase in the Leg-of-Mutton Pond (*pH* 4·0–5·0) a number of characteristic algae occur and phytoplankton is completely absent, whereas in the less acid phase (*pH* 5·5–7·0) planktonic algae (Peridineae, Chrysophyceae) are present.

The change in *pH* between the upper and lower littoral regions of the Pen Ponds is very sudden, taking place within about 1 m. In cultures of deposits from the littoral areas the *pH* nearly always falls rapidly until extremely acid conditions arise (*pH* as low as 3·6).

A number of the algae appear to be markedly acid-loving, only occurring in abundance when the *pH* is less than 5·0, viz. *Chlamydomonas longistigma*, *Scourfieldia complanata*, *Characium Pringsheimii*, *Hormidium subtile*, *Mougeotia viridis*, *Chromulina aerophila* n.sp. forma B, *Euglena mutabilis*. *Chromulina ovalis* likewise appears to favour acid conditions, though it did not disappear from the bottom flora of the Leg-of-Mutton Pond until after the summer rise in *pH* began. A few other algae appear to be wholly unaffected by the reaction of the water; *Fragilaria construens*, *Scenedesmus abundans*, *S. longus* and *S. quadricauda* occurring commonly or even abundantly through a range of *pH* from 4·2 to 9·2, and *Oscillatoria tenuis*, *O. princeps*, *Pinnularia viridis* and *P. maior* through a range of 4·5–7·5.

### (3) Plankton

These algae either possess aids to flotation or are of minute dimensions (nannoplankton) or, on the other hand, are free swimming. A number are bottom-living or planktonic, according to the area in which they occur. The Euglenineae, which are mainly found near

the bottom deposit in the upper littoral of the Pen Ponds and in area A of the Leg-of-Mutton Pond<sup>1</sup> are mainly planktonic in the Clay Pit. The possible reasons for such variations have already been discussed (p. 273). The cultures suggest that the upper littoral regions are unsuitable for the development of truly planktonic forms (*loc. cit.*). Such forms as *Synura*, *Dinobryon* and *Mallomonas* form cysts which are found in the bottom deposits throughout the year and no doubt give rise to the next phase. Cysts of *Chrysococcus*, on the other hand, are unknown and it seems likely that it persists as isolated individuals. In the Pen Ponds it occurs throughout the year, in abundance in winter and early spring and in smaller numbers and mainly as a bottom-living form during the rest of the year.

Chlorococcales are never common, but *Pediastrum boryanum* and species of *Scenedesmus* are more frequent on the bottom than in the surface layers. *Surirella* and *Cymatopleura*, which occur in the plankton of some waters are, in these ponds, confined to the bottom. Planktonic Myxophyceae (*Anabaena flos-aquae*, *Microcystis aeruginosa*) were never found on the bottom.

#### (4) Adaptations to habitat

The frequent disturbance of the surface layers of the substratum in the littoral (including both upper and lower littoral) regions has been repeatedly referred to. Sand particles, by virtue of their size and weight, are least affected, but sand is only exposed in those areas (e.g. D, F) where wave action is so frequent and strong that accumulation of the lighter organic deposits does not occur. The advantages derived from the presence of a less mobile substratum are more than nullified by the physical factors conditioning its occurrence, and sandy areas are the most barren of all.

The main factors causing disturbance of the substratum are wind and the consequent wave action, rain, animals and human beings. The larger and the more open the aspect of a body of water, the greater is the importance of wave action; thus the Clay Pit is the least affected, while the Pen Ponds are most exposed to this factor. The disturbance of the finer particles due to heavy rain is often combined with that due to wind. Water-fowl are of some importance, but small aquatic animals (water-beetles, aquatic worms, the larger Crustacea, etc.) do not appear to play any important role.

Owing to the frequent operation of one or more of these factors, the algae living on the bottom are often in danger of being buried. It is, therefore, noteworthy that with few exceptions the species living on or in close relation to the bottom deposits possess means of reaching the surface. Considered from this point of view, the species constituting the bottom flora can be grouped as follows:

- (i) Free-swimming forms, including nearly all the flagellates (except a few creeping forms like *Euglena mutabilis*).
- (ii) Forms having the capacity to perform creeping movements. Nearly all the important bottom-living diatoms (except *Fragilaria construens*) are members of the Raphidioideae. The desmids (*Closterium*, *Cosmarium*, *Pleurotaenium*, etc.) are able to perform slow movements by excretion of mucilage (Kol, 1927; Klebs, 1886). *Oscillatoria* and *Anabaena* (especially the hormogones) are capable of gliding movements. *Holopedium geminatum* exhibits slow movements, being the first colonial blue-green alga in which this has been observed (Lund, *in the press*). *Spirogyra nitida* (see Langer, 1930; Chesterman & Foster, 1936) exhibits a characteristic movement, the mechanism of which is as yet

<sup>1</sup> The shallow water in these areas tends to obscure this fact.

unexplained. When buried, a large proportion of the filaments can creep up to and even above the surface, where they appear as twisted bundles. Neither here, nor in *Holopedium geminatum*, is there any tendency to move towards the source of illumination. The *Mougeotia*, which occurs commonly on the bottom in the Upper Pen Pond, however, affords no evidence of movement.

(iii) Forms possessing mechanisms increasing buoyancy. The flotation devices common to many plankton forms must also be of value in relation to the bottom-living habit. When the deposit is disturbed such forms, since they sink more slowly than the non-living particles, will tend to accumulate in the surface layers. Certain algae of this type, commonly found in the plankton of lakes and ponds, occur occasionally on the surface of the deposits, notably *Pediastrum boryanum* and spinous species of *Scenedesmus*; the hollow colonies of *Coelosphaerium limnicolum* n.sp. (Lund, in the press) should possibly also be included here.

A number of the bottom-living algae play a role in binding the particles of the substratum and thus in forming a surface which is more resistant to disturbance. Good examples are afforded by the *Oscillatorias* which often cover the surface of the deposit with a loose mat. In the sandy areas *Scenedesmus antennatus* binds the sand grains together by means of the mucilage pads found on the tips of the spines of the end-cells of the colony, as has already been described by Chodat (1920-1936) and Scourfield (1928-9). The latter suggests that this may render the colonies a less easy prey for aquatic animals, such as Entomostraca, but it seems more likely that the importance of this habit may lie in stabilization of the substratum. *Scenedesmus antennatus* mainly occurred in the sandy areas where wave action was most severe. The same habit is shown by *Microcystis parasitica*, in which the mucilage surrounding the colonies always includes a number of sand grains partly attached to its surface.

Certain species (e.g. *Scenedesmus longus* and other species of the genus, *Fragilaria construens*) appear to have no definite means of avoiding burial, although they occur in intimate connexion with the surface particles. The species of *Scenedesmus* almost always show fine adhering particles apparently intermingled with the mucilage surrounding the colonies. This may result in an increase of surface in proportion to bulk and consequently a slower rate of sinking, since the included particles are small and light. These species of *Scenedesmus* do not bind the particles of the substratum, and occur commonly in the plankton after there has been disturbance of the deposits. They are abundant only in the least disturbed areas.

The lack of attached algae on the bottom deposits is probably largely due to frequency of disturbance and the perishable nature of many of the particles. Glass slides placed on or near the surface of the deposits often acquired an abundant coating of attached forms. In the gravel regions of the Pen Ponds there is often a rich epilithic flora, especially on the bigger, more stable, particles. Even the larger sand grains, which, as a result of their size and weight, are not obtained in suction samples, sometimes bear a few algae.

A number of filamentous algae escape burial, since they sooner or later become entangled with the surrounding macrophytes. *Spirogyra nitida*, which possesses the capacity for movement (p. 275), on the other hand occurs in areas which are largely devoid of macrophytes.

V. CONCLUSIONS<sup>1</sup>

The present investigation shows that the bottom deposits in the littoral regions of ponds bear a growth of algae on or in close proximity to the surface. This algal flora constitutes a separate community, independent of and not recruited either from the planktonic or epiphytic communities. Occasional observations on the littoral regions of other ponds (Richmond Park, Epping Forest, Yorkshire, Derbyshire and the Lake District) show that similar floras are of widespread occurrence.

The presence or absence of such a bottom-living community is determined by the degree of stability of the deposit and this, in turn, depends on its position. Shallow exposed areas (D and F) are barren owing to frequent disturbance and the non-deposition of organic litter. Disturbance, especially of the light organic particles, occurs also, however, in the more sheltered areas. It is, therefore, significant that almost all the algae constituting these communities are capable of movement by one means or another. The few exceptions have been discussed on p. 276.

The structure, depth and percentage organic content of the deposits vary from pond to pond, in different areas of the same pond and even in the same area at different times of the year. With high organic content, great depth of deposit and marked stagnation, Euglenineae and certain other flagellates become predominant on the submerged deposits, while certain pennate diatoms and species of *Oscillatoria* become dominant on the uncovered deposits in summer and autumn. Such deposits are to be found in the Clay Pit and in the upper littoral of the Pen Ponds (areas C and E). The floras occurring in the submerged and uncovered parts of these areas are similar. In the Pen Ponds the maxima only developed in the summer and autumn (see pp. 261, 264 and Table 1, pp. 256-9), but in the Clay Pit the maximum is reached in late autumn and the algae concerned are more or less commonly present throughout the year. The basic similarity of these areas is further emphasized by the results of cultures in the laboratory. Occasional examination of similar types of deposits in other parts of these ponds shows that they bear comparable floras.

Where the deposits contain little organic matter and are of slight depth, other types of flora occur. The deposits containing least organic matter are those of the most exposed upper littoral regions of the Pen Ponds (i.e. areas D, F) and these are very barren. In the deeper, lower littoral, regions of areas C and E also the organic content is very low and here Euglenineae and other flagellates are very rare and sporadic (Table 1). The floras of these lower littoral areas differ markedly from those of the upper littoral and also, to some extent, from one another. They are dominated by pennate diatoms (different species to those of the upper littoral) accompanied by *Caelosphaerium limnicolum* n.sp. and *Holopedium geminatum* in the Upper and *Spirogyra nitida* in the Lower Pond. Area A (Leg-of-Mutton Pond) is intermediate in organic content and flora between the more organic areas (Clay Pit, upper littoral of areas C and E) and area B, which shows similarity to the lesser organic areas (lower littoral of areas C and E) in the presence of *Scenedesmus longus* and other species of the genus and *Fragilaria construens*.

A number of other factors affect the flora of the deposits, such as seasonal variation in exposure and disturbance, variation in the nature of the deposits themselves in the course of the year (areas C and E), variation in rainfall from year to year and in the course of the year, and variation in hydrogen-ion concentration. The Leg-of-Mutton Pond is

<sup>1</sup> Reference to Table 1, pp. 256-9, will illustrate many of the points here mentioned.

extremely acid during winter and early summer when it shows a complete absence of phytoplankton and an abundant growth of *Scourfieldia complanata* and *Chromulina ovalis* close to the surface of the deposit, often visible to the naked eye.

The various marginal deposits (except from areas D and F) possess the capacity, without enrichment, to produce a flora containing the majority of the algae found in those areas in nature, only the planktonic algae being absent. This has been established by covering samples of the deposit with distilled water. The succession of floras occurring in nature are not the result of artificial pollution. The undecomposed deposits from the Clay Pit and upper littoral of the Pen Ponds undergo similar changes in the cultures to those occurring in nature, and the flora exhibits a comparable succession. The deposits from the lower littoral regions of the Pen Ponds, on the other hand, do not show this capacity, and it is suggested that their natural flora depends on the continual addition of silt from the plankton and elsewhere. The cultures of deposits from the Leg-of-Mutton Pond do not show a clear succession of algae, nor is there any difference in the behaviour of deposits from the marginal and central regions.

The marginal and upper littoral deposits are therefore of great importance in nature, and their constitution controls, to a large extent, the type of flora that can occur on them. This finds support in the fact that in the Pen Ponds the upper littoral deposits produce the typical flora in greatest abundance in summer and autumn, when they are least affected by external factors such as disturbance and admixture with the water of the main pond.

In general it appears that the smaller a body of water, the more important will the bottom deposit be as a factor controlling the flora of the whole pond. This is due to the fact that, apart from rainfall, there is less water introduced from other sources and, owing to the slight depth, the products of decay of the bottom deposit are more readily available to the pond as a whole than in a lake. The more sheltered marginal regions of larger ponds (e.g. Pen Ponds) and lakes constitute a separate habitat of similar importance, producing an analogous flora for the same reason. In the deeper regions of such waters the rate of decay of the bottom materials and the rate at which their decomposition products become available to the body of water above them is extremely slow, and the influence of the water flowing in from the larger drainage area becomes of greater importance. Occasional observations made elsewhere support this view. The presence or absence of nearby trees is a very important factor in controlling the type of bottom deposit in small ponds and in the marginal areas of larger ponds and lakes.

While the biological importance of the deposits on the bottom of a lake has long been more or less clearly recognized, the greater availability of the products of the deposits in the shallow littoral regions and hence their more immediate availability to the supernatant and surrounding water appears to have been overlooked.

It is principally the deeper deposits of lakes that have so far been studied (see Fritsch, 1931, pp. 235-7) and they do not appear to be altogether comparable to those dealt with here. The works of Godward (1937), Hurter (1928), Hustedt (1923), Koppe (1923) and Utermöhl (1923, 1925) afford but few data of interest from the present point of view. Godward (pp. 511-12), describing the bottom communities on dead leaves between 0 and 16 m., enumerates a number of diatoms (*Navicula rhyncocephala* and other species of the genus, *Nitzschia palea*, *N. sigmoidea*, *Pinnularia gibba*, *P. mesolepta*, *Stauroneis anceps*, *S. phoenicentron*, *Surirella robusta*) which occur also on the deposits here described.

Hurter and Hustedt describe similar communities. Hustedt (1923, p. 100) describes three not clearly demarcated zones in the diatom flora of lakes, viz. the zone of littoral sediments, that of the deep-water forms, and lastly the remainder of the bottom, which is the region of pelagic sedimentation. Among the deep-water forms he mentions several species present in the lower littoral of the Pen Ponds, viz. species of *Cymatopleura*, *Camptodiscus*, *Gyrosigma*, *Neidium*. According to him, the smaller and shallower lakes harbour immense quantities of the smaller species of *Fragilaria* (cf. *F. construens*). Hurter mentions the presence of *Surirella* on the bottom. Utermöhl studied lakes rich in humus sediments ('Humusschlammseen') resulting from the presence of numerous dead leaves. He is mostly concerned with the plankton, which is rich in flagellates, including some (*Chromulina*, *Chrysococcus*, *Mallomonas*, *Euglena*) that occur in the Clay Pit and upper littoral of the Pen Ponds. The water near the bottom, at a greater depth than in the areas here studied, is in his lakes dominated by colourless saprophytic organisms.

## VII. LIST OF ALGAE IDENTIFIED

The large number of algae included, despite the small size of the area, gives some idea of the richness and variety of the flora. A considerable number of new or little-known forms have been observed and are described elsewhere (Lund, in the press), the discovery of which is no doubt due to the study of a new habitat. The customary mode of occurrence of each species is indicated by the following symbols: *b*, bottom-living, *e*, epiphytic, and *p*, planktonic. Some species vary in their mode of occurrence in different areas (e.g. Euglenineae in the Clay Pit and upper littoral of the Pen Ponds), for which see the main text. Where only a few specimens have been observed, no symbol is given. The classification followed is that of Fritsch (1935) and Fritsch & West (1927).

### CHLOROPHYCEAE

#### VOLVOCALES

- Carteria cordiformis* (Carter) Dill
- C. crucifera* Korsch.
- C. globosa* Korsch.
- C. multifilis* Dill (*b*)
- Chlamydobotrys gracilis* Korsch. (*b*)
- Chlamydomonas acuta* Korsch. (*b*)
- C. cingulata* Pascher (*b*)
- C. longistigma* Dill (*b*, *p*)
- C. microscopica* G. S. West (*b*)
- C. minutissima* Korsch. (*b*)
- C. oblonga* Anachin (*b*, *p*)
- C. parietaria* Dill (*b*)
- C. Reinhardi* Dang. (*b*)
- C. Westiana* Pascher (*b*)
- Coccomonas orbicularis* Stein (*b*)
- Eudorina elegans* Ehrenb. (*b*, *p*)

#### CHLOROCOCCALES

- Ankistrodesmus falcatus* (Corda) Ralfs (*p*)
- A. falcatus* f. *duplex* (Kütz) G. S. West (*p*)
- A. falcatus* f. *acicularis* (A. Braun) G. S. West (*p*)
- Characium Pringsheimii* A. Braun (*e*)
- C. falcatum* Schroed. (*e*)
- Chlorella vulgaris* Beij.

- Gonium pectorale* Müller (*b*, *p*)
- G. sociale* Warming
- Heteromastix angulata* Korsch. (*b*)
- Mesostigma viride* Laut. (*b*)
- Palmodictyon varium* (Naeg.) Lemm. (*e*)
- Pandorina morum* Bory (*b*)
- Polytoma uvella* Stein (form) (*b*)
- Pteromonas angulosa* Lemm. (*b*)
- Pyramimonas delicatula* Griff.
- Schizochlamys delicatula* G. S. West
- Scourfieldia complanata* G. S. West (*b*)
- Spermatozopsis exultans* Korsch. (*b*)
- Sphaerobotrys fluvialis* Butcher (*e*)
- Volvox aureus* Ehrenb. (*b*, *p*)
- V. globator* (L.) Ehrenb. (*b*, *p*)
- V. tertius* A. Meyer (*b*, *p*)

- Chlorococcum infusionem* (Schrank.) Menegh.
- Chlorochytrium Lemnae* Cohn
- Coelastrum microporum* Naeg. (*p*)
- C. proboscideum* Bohl. (*p*)
- Desmatractum bipyramidatum* (Chod.) Pascher (*b*)
- Dictyosphaerium Ehrenbergianum* Naeg. (*p*)

**CHLOROCOCCALES (continued)**

- D. pulchellum* Wood (p)  
*Kirchneriella lunaris* (Kirch.) Moeb. (p)  
*Lagerheimia genevensis* Chod. (p)  
*Pediastrum boryanum* (Turp.) Menegh. (p)  
*P. duplex* Meyen (p)  
*P. duplex* var. *clathratum* A. Braun (p)  
*P. tetras* (Ehrenb.) Ralfs (b, p)  
*Scenedesmus abundans* (Kirch.) Chod.  
*S. antennatus* Bréb. (b)  
*S. armatus* (Chod.) G. M. Smith (b)

**ULOTRICHALES**

- Enteromorpha intestinalis* Link. (e)  
*Hormidium subtile* (Kütz.) Heer. (e)  
*Microspora stagnorum* (Kütz.) Lagerh. (e, b)  
*Ulothrix zonata* (Web. et Mohr.) Kütz (e)

**CLADOPHORALES**

- Cladophora glomerata* (L.) Kütz. (e)  
**OEDOGONIALES**

- Bulbochaete subintermedia* Elfv. (e)

**CONJUGALES**

- Arthrodesmus incus* (Bréb.) Hass. var. *minor* W. & G. S. West (e, b)  
*Closterium Jenneri* Ralfs (e, b)  
*C. juncidum* Ralfs (e, b)  
*C. Kützingii* Bréb. (e, b)  
*C. Kützingii* var. *onychosporum* G. S. West  
*C. Leibleinii* Kütz. (b)  
*C. navicula* (Bréb.) Lutk. (e, b)  
*C. pronum* Bréb. (e, b)  
*C. rostratum* Ehrenb. (e, b)  
*C. Malvinacearum* De Not. (b)  
*C. striolatum* Ehrenb. (b)  
*Mougeotia viridis* (Kütz.) Wittrock (e, b)  
*Spirogyra nitida* (Dill) Link. (b)

- Botryococcus Brauni* Kütz. (e)  
*Mischococcus confervicola* Naeg. (e)  
*Tribonema affine* G. S. West (e)

- Bicoeca planktonica* Kisselaw (p)  
*Chromulina aerophila* n.sp. (b)  
*C. ferrea* n.sp. (b)  
*C. ovalis* Klebs (b)  
*C. sporangifera* n.sp. (e, b)  
*Chrysamoeba radians* Klebs (e, b)  
*Chrysidiastrum catenatum* Laut. (p)  
*Chrysococcus rufescens* Klebs var. *tripora* n.var. (p)  
*Chrysopyxis globosa* Stein (e)  
*Dinobryon divergens* Imhof (p)  
*D. divergens* var. *angulatum* (Sel.) Brunn. (p)  
*D. sertularia* Ehrb. (p)  
*D. (Epipyxis) utriculus* Stein (e)  
*Heterolagynion Oedogonii* Pascher (e)  
*Hyalobryon ramosum* Laut. (e)

- S. bijuga* (Turp.) Lag. (b)  
*S. bijuga* var. *alternans* (Reinsch) Hansg. (b)  
*S. dimorphus* (Turp.) Kütz. (b)  
*S. longus* Meyen (b)  
*S. longus* var. *Nægeli* Smith (b)  
*S. serratus* (Corda) Bohl. (b)  
*S. quadricauda* (Turp.) Bréb. (b)  
*Tetraedron limneticum* Borge (p)  
*T. Schmidlei* (Schroed.) Lemm. (p)  
*Tetrastrum staurogeniaeforme* (Schroed.) Lemm. (p)

**CHAETOPHORALES**

- Aphanochaete repens* A. Braun. (e)  
*Chaetophora elegans* (Roth.) Ag. (e)  
*C. incrassata* (Huds.) Hazen. (e)  
*Chaetosphaeridium globosum* (Nordst.) Klebahn (e)  
*Coleochoaete scutata* Bréb. (e)  
*Dicranochaete reniformis* Hieron. (e)  
*Microthamnion Kützingianum* Kütz. (e)  
*Stideoclonium tenue* Kütz. (e)  
*Ulvella frequens* Butcher (e)

- C. venus* Kütz. (b)  
*Cosmarium bioculatum* Bréb. (e, b)  
*C. Meneghinii* Bréb. (e, b)  
*C. Regnesi* Reinsch (e, b)  
*C. Turpinii* Bréb. (e, b)  
*Micrasterias denticulata* Bréb. (e, b)  
*M. rotata* (Grev.) Ralfs (e, b)  
*Pleurotaenium Trabecula* (Ehrenb.) Naeg. (b)  
*Staurastrum dejectum* Bréb. var. *patens* Nordst. (e, b)  
*S. inflexum* Bréb. (e, b)  
*S. lunatum* Ralfs (e, b)  
*S. paradoxum* Meyen (e, b)  
*Zygnum cruciatum* (Vauch.) Ag. (b)

**XANTHOPHYCEAE**

- Botrydiopsis arrhiza* Borzi (e)  
*Ophiocytium arbuscula* Rabenh. (e)

**CHRYSOPHYCEAE**

- Lagynion Scherffelii* Pascher (e)  
*Kephyrion littorale* n.sp. (p)  
*K. littorale* var. *constricta* n.var. (p)  
*Mallomonas akromonas* Ruttner (p)  
*M. heterospina* n.sp. (p)  
*M. intermedia* Kisselaw (p)  
*M. limnicola* n.sp. (p)  
*M. radians* Conrad var. *ovalis* n.var. (b)  
*Naegeliella britannica* Godward (e)  
*Ochromallomonas pelophila* n.gen., n.sp. (b)  
*Pseudomallomonas anglica* Carter (b)  
*Sphaleromantis ochracea* Pascher (b)  
*Synura uvella* Ehrenb. (p)  
*Uroglenopsis americana* Lemm. (p)

## BACILLARIOPHYCEAE

- Attheya Zachariasii* J. Brun. (p)  
*Cyclotella comta* (Ehrenb.) Kütz. (p)  
*Melosira granulata* (Ehrenb.) Ralfs (b)  
*Rhizosolenia morsa* W. & G. S. West (p)  
*Stephanodiscus Hantzschii* Grun. (p)

*Achnanthes minutissima* Kütz. (e)  
*A. minutissima* var. *cryptocephala* Grun. (e)  
*Amphipleura pellucida* Kütz. (b)  
*Amphora ovalis* Kütz. (b)  
*Asterionella formosa* Hassall (e)  
*A. gracillima* (Hantzsch.) Heib. (e)  
*Caloneis silicula* (Ehrenb.) Cleve (b)  
*Campyloidiscus noricus* Ehrenb. var. *hibernica* (Ehrenb.) Grun. (b)  
*Coccneis placentula* Ehrenb. (e)  
*C. placentula* var. *euglypta* (Ehrenb.) Cleve (e)  
*C. pediculus* Ehrenb.  
*Cymatopleura elliptica* (Bréb.) W. Smith  
*C. elliptica* var. *hibernica* (W. Smith) Hust. (b)  
*C. elliptica* var. *nobilis* (Hantzsch.) Hust. (b)  
*C. solea* (Bréb.) W. Smith (b)  
*C. solea* var. *regula* (Ehrenb.) Grun. (b)  
*Cymbella Ehrenbergii* Kütz. (b)  
*C. lanceolata* (Ehrenb.) Van Heurck (b)  
*C. ventricosa* Kütz. (b)  
*Diatoma vulgare* Bory (e)  
*Epithemia argus* Kütz.  
*E. zebra* (Ehrenb.) Kütz. var. *porcellus* (Kütz.) Grun. (e)  
*Eunotia arcus* Ehrenb. (e)  
*E. lunaris* (Ehrenb.) Grun. (e)  
*E. lunaris* var. *capitata* Grun. (e)  
*E. lunaris* var. *subarcuata* (Naeg.) Grun. (e)  
*Fragilaria capucina* Desm. (e)  
*F. construens* (Ehrenb.) Grun. (b)  
*F. construens* var. *venter* (Ehrenb.) Grun. (b)  
*Gomphonema acuminatum* Ehrenb. (e)  
*G. acuminatum* var. *coronata* (Ehrenb.) W. Smith (e)  
*G. constrictum* Ehrenb. (e)  
*G. parvulum* (Kütz.) Grun. (e)  
*Gyrosigma acuminatum* Kütz. (b)  
*Navicula cryptocephala* Kütz. (b)  
*N. cuspidata* Kütz. (b)  
*N. cuspidata* var. *ambigua* (Ehrenb.) Cleve (b)  
*N. dicephala* (Ehrenb.) W. Smith (b)  
*N. pupula* Kütz. (b)  
*N. pupula* var. *capitata* Hust. (b)  
*N. hungarica* Grun. (b)  
*N. hungarica* var. *capitata* (Ehrenb.) Cleve (b)  
*N. minima* Grun. (b)

*N. rhyncocephala* Kütz. (b)  
*Neidium iridis* (Ehrenb.) Cleve (b)  
*N. productum* (W. Smith) Cleve (b)  
*Nitzschia flexa* Schum. (b)  
*N. acicularis* W. Smith (p)  
*N. dissipata* (Kütz.) Grun. (b)  
*N. dubia* W. Smith (b)  
*N. gracilis* Hantzsch. (b)  
*N. hungarica* Grun. (b)  
*N. ignorata* Krasske (b)  
*N. Kützingiana* Hilse (b)  
*N. palea* (Kütz.) W. Smith (b)  
*N. recta* Hantzsch. (b)  
*N. sigmaidea* (Ehrenb.) W. Smith (b)  
*N. stagnorum* Rabh. (b)  
*N. Tryblionella* Hantzsch. (b)  
*N. Tryblionella* var. *victoriae* Grun. (b)  
*N. vermicularis* (Kütz.) Grun. (b)  
*N. acuta* Hantzsch. (b)  
*Pinnularia gibba* Ehrenb. (b)  
*P. gibba* f. *linearis* Hust. (b)  
*P. interrupta* W. Smith (b)  
*P. interrupta* f. *minutissima* Hust. (b)  
*P. maior* (Kütz.) Cleve (b)  
*P. mesolepta* (Ehrenb.) W. Smith (b)  
*P. microstauron* (Ehrenb.) Cleve (b)  
*Rhoicosphenia curvata* (Kütz.) Grun. (e)  
*Rhopalodia gibba* (Ehrenb.) O. Müll. (e)  
*Stauroneis acuta* W. Smith (b)  
*S. anceps* Ehrenb. (b)  
*S. anceps* f. *gracilis* (Ehrenb.) Cleve (b)  
*S. anceps* f. *linearis* (Ehrenb.) Cleve (b)  
*S. phoenicentron* Ehrenb. (b)  
*Surirella biseriata* Bréb. (b)  
*S. biseriata* var. *bifrons* (Ehrenb.) Hust. (b)  
*S. Capronii* Bréb. (b)  
*S. elegans* Ehrenb. (b)  
*S. linearis* N. Smith (b)  
*S. linearis* f. *constricta* (Ehrenb.) Grun. (b)  
*S. óvata* Kütz. (b)  
*S. robusta* Ehrenb. (b)  
*S. robusta* var. *splendida* (Ehrenb.) Van Heurck. (b)  
*S. spiralis* Kütz. (b)  
*Synedra amphicephala* Kütz.  
*S. parasitica* (W. Smith) Hust. (e)  
*S. parasitica* var. *sub-constricta* Grun. (e)  
*S. pulchella* Kütz. (e)  
*S. ulna* (Nitzsch.) Ehrenb. (e)  
*S. ulna* var. *amphirhyncus* (Ehrenb.) Grun. (e)

CRYPTOPHYCEAE

- Chilomonas paramaecium Ehrenb. (b)**  
**Chroomonas Nordstedtii Hansg. (b)**

- ### Cryptomonas spp. (b, p)

## DINOPHYCEAE

- Ceratium hirundinella* Schrank. (*p*)  
*Glenodinium uliginosum* Schill. (*p*)  
*Gymnodinium aeruginosum* Stein. (*p*)  
*G. vorticella* Stein. (*p*)

- Heminidium nasutum* Stein. (*p*)  
*Peridinium cinctum* (O. Müll.) Ehrenb. (*p*)  
*P. marchicum* Lemm. (*p*)

EUGLENINEAE<sup>1</sup>

- Colacium vesiculosum* Ehrenb. (*e*)  
*Euglena acus* Ehrenb.  
*E. acus* var. *hyalina* Klebs.  
*E. caudata* Hübner.  
*E. fusca* (Klebs) Lemm.  
*E. geniculata* Duj.  
*E. intermedia* (Klobes) Schmitz.  
*E. intermedia* var. *Klebsii* Lemm.  
*E. mutabilis* Schmitz (incl. *E. Klebsii* Mainx)  
*E. pisciformis* Klebs  
*E. pisciformis* var. *minor* Hansg.  
*E. oxyuris* Schmarda  
*E. sanguinea* Ehrenb.  
*E. spirogyra* Ehrenb.  
*E. spirogyra* var. *marchica* Lemm.  
*E. tripteris* (Duj.) Klebs  
*E. variabilis* Klebs  
*E. velata* Klebs  
*E. viridis* Ehrenb.  
*Eutreptia viridis* Perty.  
*Lepocinclis ovum* (Ehrenb.) Perty.  
*L. salina* Fritsch  
*L. Steinii* Lemm.  
*L. teres* (Schmitz) Francé  
*Phacus acuminata* Stokes  
*P. aenigmatica* Drez.  
*P. agilis* Skuja  
*P. alata* Klebs var. *latviensis* Skvortz.  
*P. caudata* Hübner

- P. hispidula* (Eichw.) Lemm.  
*P. longicauda* (Ehrenb.) Duj.  
*P. longicauda* var. *ovata* Skvortz.  
*P. longicauda* (Ehrenb.) Duj. var. *torta* Lemm.—  
*P. torta* (Lemm.) Skvortz.  
*P. oscillans* Klebs  
*P. parvula* Klebs  
*P. pleuronectes* (O.F.M.) Duj.  
*P. pleuronectes* var. *hyalina* Klebs  
*P. pusilla* Lemm.  
*P. pyrum* (Ehrenb.) Stein  
*P. triqueter* (Ehrenb.) Duj.  
*Trachelomonas abrupta* Swir. var. *minor* Defl.  
*T. acanthostoma* (Stokes) Defl.  
*T. acuminata* (Schm.) Stein  
*T. armata* (Ehrenb.) Stein  
*T. bulla* (Stein) Defl.  
*T. caudata* (Ehrenb.) Stein  
*T. hispida* (Perty) Defl.  
*T. hispida* f. *cylindrica* Klebs  
*T. hispida* f. *coronata* Lemm.  
*T. intermedia* Dang.  
*T. oblonga* Lemm. var. *truncata* Lemm.  
*T. rugulosa* (Stein) Defl.  
*T. tambowiaka* Swir.  
*T. varians* Defl.  
*T. varians* f. *minor* n.f.  
*T. varians* f. *spiralis* Defl.  
*T. volvocina* Ehrenb.

## MYXOPHYCEAE

- Aphanothecce stagnina* (Spreng.) A. Braun (*b*)  
*Coelosphaerium limnicolum* n.sp. (*b*)  
*Gomphosphaeria lacustris* Chod. (*p*)  
*Holopodium geminatum* Lagerh. (*b*)  
*Marssonella elegans* Lemm. (*b*)  
*Merismopedia elegans* A. Braun (*b*)  
*M. glauca* (Ehrenb.) Nág. (*b*)  
*Microcystis aeruginosa* Kütz. (*p*)  
*M. parasitica* Kütz. (*b*)  
*Chamaesiphon incrustans* Grun. (*e*)

- Anabaena catenula* (Kütz.) Born var. *affinis* (Lemm.) Geitl. (*p*)  
*A. cylindrica* Lemm. (*b*)  
*A. flos-aquae* (Lyng.) Bréb. (*p*)  
*A. oscillarioides* Bory (*b*)  
*Cylindrospermum alatosporum* F. E. Fritsch (*b*)  
*Gloetrichia natans* Rab. (*e*)  
*Oscillatoria limosa* Ag. (*b*)  
*O. princeps* Vauch. (*b*)  
*O. splendida* Grev. (*b*)  
*O. tenuis* Ag. (*b*)  
*Tolyphothrix tenuis* (Kütz.) J. Schmidt (*e, b*)

The author's grateful thanks are due to Prof. F. E. Fritsch, F.R.S., for his valuable help and criticism.

<sup>1</sup> All, except *Colacium*, may be bottom-living or planktonic according to habitat (see p. 275).

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# THE INFLUENCE OF THE MINERAL COMPOSITION OF THE MEDIUM ON THE GROWTH OF PLANKTONIC ALGAE

## PART I. METHODS AND CULTURE MEDIA

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(*With eight Figures in the Text*)

### I. INTRODUCTION

Various factors have been taken into consideration to explain the periodicity and distribution of phytoplankton during the last 50 years. These include temperature, sunshine, vertical circulation of the water, rainfall and flood, dissolved substances in the water, and the nature of the geological formation. All of these, except the first two, influence the growth of phytoplankton mainly through the effect of the substances dissolved in the water. Numerous attempts have been made to correlate the occurrence of planktonic organisms with one or other factor, but all have met with serious criticism in one respect or another. Owing to the complex interrelations of the factors and the numerous physical and chemical reactions involved, which are, moreover, complicated by biotic interactions of the different organisms, it scarcely seems possible to arrive at any definite conclusions on the basis of field observations or on cultures with enriched natural water, unless these are checked by controlled laboratory experiments.

The more important planktonic organisms have never been successfully cultivated in artificial media consisting only of pure chemicals in known concentrations, and hence an experimental investigation of the factors influencing their development, though long recognized as essential, has been impossible. As a result of the failure to grow these organisms in synthetic media, there was a general belief that unknown substances present in natural waters were essential for successful growth. Many workers obtained satisfactory growth by the addition of soil extract whereby, however, an unknown factor was introduced.

Solutions of pure chemicals, similar in composition and concentration to those occurring in natural waters, are essential if the effect of varying the concentration of a salt is to be investigated. Efforts were therefore specially directed at the beginning of the present work towards the preparation of media, which would imitate different types of natural water as closely as possible. Artificial solutions, based on the normal composition of natural waters, were prepared after numerous experiments, so that ultimately all the planktonts that could be isolated were successfully grown in cultures. The growth was often better than that occurring in nature, where there are always some unfavourable factors.

Temperature, within normal limits, has little direct effect on the development of the planktonts studied, but light intensity is of greater importance. Growth is always favourably affected by increase of light within natural limits. The writer's experiments are therefore concerned solely with the effect of the chemical composition of the medium under suitable conditions of illumination, these two factors being regarded as of the greatest importance in relation to plankton growth.

Though a considerable number of planktonic algae were isolated and successfully cultivated, only six are dealt with in any detail in the following account, namely, two Chlorophyceae (*Pediastrum*, *Staurastrum*), a member of Xanthophyceae (*Botryococcus*) and three diatoms (*Asterionella*, *Fragilaria* and *Nitzschia*). The range of concentrations of salts used varies between zero and one approaching or exceeding that occurring in natural waters. The first part of this contribution deals with the procedure adopted in obtaining suitable culture media; the second part with the influence of the concentration of inorganic nitrogen and phosphate. The effect of varying the concentration of other important mineral constituents has also been investigated, and some reference is made to the results in § IV: the full data will be communicated later.

## II. MATERIAL AND METHODS OF CULTURE AND ISOLATION

All the material used was derived from cultures, originally started from a single cell or colony. The organisms were isolated from fresh plankton samples collected from artificial ponds (*Pediastrum*, *Botryococcus*), from a stream in the Botanic Garden, Cambridge (*Nitzschia palea*), from the Barn Elms Reservoir of the Metropolitan Water Board, London (*Nitzschia acicularis*, *Staurastrum*, *Fragilaria*, *Cryptomonas*), and from Lake Windermere (*Asterionella*, *Tabellaria flocculosa*, *T. fenestrata*, *Oscillatoria tenuis*). The media were prepared from British Drug House 'Analar' chemicals containing known maximum amounts of impurities,<sup>1</sup> and only Pyrex glassware was used. Monax test-tubes, which were first tried, proved to be unsatisfactory, since even after cleaning in the way described below there was still a marked solution of substances from the glass. All the results obtained with cultures in Monax tubes have therefore been discarded, since none can be considered reliable. The unfavourable effect seems to be less marked when Monax tubes are used in conjunction with agar cultures.

Pyrex test-tubes (with rim), having capacities of 20–25 and 100–110 c.c. respectively, were employed. In every given series of cultures care was taken to select tubes with the same inside and outside diameters in order to avoid differences that might affect the photoelectric estimation of the cultures.

Proper cleaning of the glassware is of great importance. Many instances of failure at the commencement of this work were partly due to insufficient cleaning. All glassware, after a preliminary rinsing in hot water, was soaked in strong potassium dichromate sulphuric acid solution for 2 days, then heated at about 70° C. for an hour, thoroughly rinsed successively with hot water, ordinary distilled water and Pyrex glass-distilled water, and finally carefully drained, avoiding contamination from dust. Even so, a few of the duplicate cultures in the smaller tubes occasionally proved to be inconsistent, which must either be due to insufficient cleaning or to impurities in the glass itself. The larger tubes were always satisfactory.

Artificial illumination was almost invariably employed. For the preliminary experiments, De's apparatus (1939, p. 128) was used at ordinary room temperature; cultures in Petri dishes and flasks were placed inside the chamber and on the covering glass plate, while test-tube cultures were suspended at different levels round the framework. This apparatus is referred to as 'A' in the subsequent matter. A second illuminating apparatus

<sup>1</sup> In the case of potassium phosphate and potassium silicate, B.D.H. 'Pure' chemicals were used, since no 'Analar' preparations of these are on the market.

'B' was used to keep cultures at a constant low temperature ( $8 \pm 1^\circ \text{C}$ .). This consisted of a refrigerator with a capacity of approximately 1 cu.m., the interior of which was illuminated by a number of evenly distributed 60 W. lamps. This apparatus was only available until August 1939, when the investigation was transferred to Cambridge. Here an illuminating apparatus 'C', in which a water current carries away the heat produced by a 500 W. lamp, was employed. This apparatus (Fig. 1), which has mainly been used during the last two years, proved to be very satisfactory.

The lamp (A) is immersed in water contained in an inverted bell-jar (B), the mouth of which is covered with a board (C) fixed to the bell-jar by clamps (D). The middle of the board carries the metal lamp-holder (M), while a hole on one side admits the glass inlet tube (E) which is of about 1 cm. bore and reaches nearly to the bottom of the bell-jar. The upper end of this tube is connected to a tap by means of pressure tubing. Two glass outlet tubes (F, G) pass through a rubber stopper (H) at the base of the jar and discharge into a sink (L). The top of one tube (G) is 1 cm., while that of the other (F) is 3 cm. below the rim of the jar, both extending to well above the bulb of the lamp. The outflow is usually taken by the tube F; the other serves to prevent an overflow, when the pressure of water is unusually high. The bell-jar rests on an iron tripod (I). The whole is surrounded by a cylinder of wire netting, about 70 cm. high, upon which the cultures are suspended at different levels. The distance between the source of light and the culture tubes thus varies between 36 cm. near the middle to roughly 61 cm. at the top and bottom. The cultures of any one experiment were invariably suspended at the same distance from the lamp. The middle part of the cylinder, with a light intensity of 3800 m.c., unless otherwise stated, was used for cultures of *Pediastrum*, *Staurastrum* and *Botryococcus*, while the higher and lower levels, with a light intensity round about 2000 m.c., were used for those of diatoms. The intervening spaces were occupied by subcultures.

One such apparatus was set up in the laboratory, while a second was placed in a constant-temperature room ( $8 \pm 0.5^\circ \text{C}$ . ) in the Department of Zoology, Cambridge, where the cultures could be illuminated continuously. After July 1940, when the cooling mechanism was no longer in operation, the temperature in the room varied from 15 to  $24^\circ \text{C}$ . The stream of water passing through the bell-jar was usually so regulated that the current just sufficed to remove the heat of the lamp, but sometimes it was adjusted to run a little more slowly so that the heat of the lamp which was not removed maintained a temperature within the wire cylinder which fluctuated less than that of the laboratory. No algal growth appeared in the water within the bell-jar, but a slight and easily removable deposit of silt formed occasionally on the upper part of the bulb.

Most of the methods used for isolating bacteria and fungi are suitable for algae. The dilution method followed by agar plate cultures, Mutch's micro-selection method, and serial cultures on agar plates (Eyre, 1930), were at first employed, but none of these proved to be very convenient or reliable. Most planktonic algae have a mucilaginous surface to which minute unicellular organisms readily adhere; the latter are sometimes lodged deeply in the gelatinous substance and difficult to eliminate.

In the later work use was made of a washing method, the procedure followed being modified from that used by Hargitt & Fray (1917), Parpart (1928) and Pringsheim (1936) for Protozoa. All apparatus and media are sterilized beforehand. The sample containing the organism required is, according to the density of the population, diluted from three to five times in succession with a suitable medium (generally medium 2, 9 or 12 for dia-

toms and blue-green algae; 10 or 11 for others, see p. 298), the tube being violently shaken before each dilution. An individual or colony is then picked out under a binocular dissecting microscope with a capillary pipette and transferred to the first of the ten drops of medium, nine of which are arranged in a circle in a Petri dish, whilst the tenth is in the centre. The tips of the pipettes are drawn out so as to be just large enough to accommodate the particular organism and are smoothed over a small flame. The other end is plugged with cotton-wool and fitted with a strong rubber teat punctured by a small hole. Frequently the spontaneous rise of the medium in the pipette by capillarity is more than sufficient without applying suction and the extent of this rise can be checked by placing the thumb over the hole in the teat. The individual or colony is washed by successive transference from drop to drop, a new pipette being used each time. After the introduction

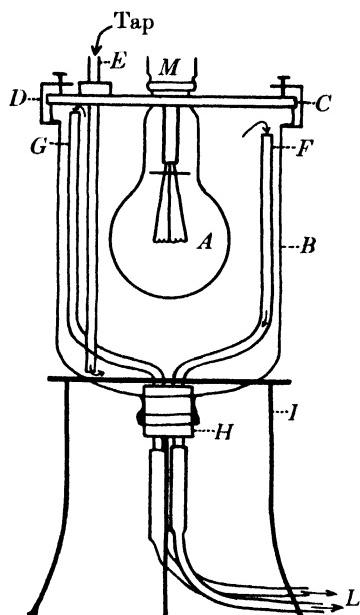


Fig. 1. Illuminating apparatus 'C'.

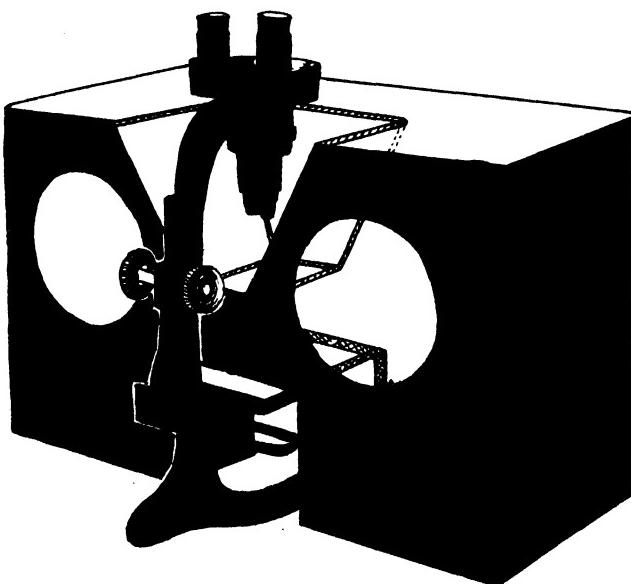


Fig. 2. Binocular isolating chamber with the binocular microscope fitted outside, showing the concavities accommodating the draw tube and the base of the microscope.

of the organism the drop is violently agitated by blowing in air with the pipette; in this way the alga is thoroughly washed before transference to the next drop.

The whole process of washing is carried out in the isolating chamber (Fig. 2) and generally occupies about 10 min., although more time is needed with organisms like *Botryococcus* which possess a large amount of mucilage; here prolonged agitation is necessary in order to detach the adhering foreign organisms. From the tenth drop the alga is transferred to a hollowed slide, which is filled with a suitable medium, and washed in a similar way. Five of these secondary washings usually suffice to ensure purity, although for *Botryococcus*, *Oscillatoria rubescens* and *O. tenuis* ten to fifteen slides were necessary, while individuals of *Cryptomonas ovata* washed in the first ten drops of medium already proved to be pure. This flagellate requires careful handling and gentle washing, since vigorous treatment kills it.

After the washing is complete, the organism is transferred to a culture vessel containing a larger quantity of medium. Cultures in glass boxes or on agar plates are convenient for frequent examination under the binocular microscope, but are easily contaminated, even if kept in the culture chamber of illuminating apparatus A (p. 285). Since most of the planktonic organisms do not grow so well on agar, a large proportion of the cultures were carried out in liquid media.

The isolating chamber (Fig. 2) consists of a rectangular box, 51 cm. long, 25.5 cm. wide and 30.5 cm. deep, made of sheet zinc and white enamelled on the inside. Two cavities in the front of the chamber, a V-shaped one at the top and a rectangular one at the bottom, allow cultures manipulated inside the chamber to be viewed with a binocular microscope which is entirely outside. The two cavities, as well as the top and front of the chamber, are constructed of glass on a thin framework of zinc, the upper accommodating the draw tube of the microscope and the lower the base. Cultures for examination are placed in the chamber on the top of the lower cavity which acts as the stage. Since the bottom of the upper cavity is situated between the objective and the stage, it is constructed of glass of specially good quality so that it does not appreciably interfere with the passage of light reflected from the mirror of the microscope, or cause any distortion of the image. The mirror of the microscope receives light from one of two electric lamps mounted in the back of the chamber. Of the two lamps used, one was a strip-light fixed above the level of the glass stage, while the other was an ordinary 60 W. bulb placed opposite the mirror of the microscope.

Before use the chamber is sterilized by wiping with a 0.1 % solution of  $HgCl_2$ . Both hands must be disinfected, preferably with a non-volatile substance, since flagellates like *Cryptomonas* and *Synura* are very sensitive to the vapours of volatile antiseptics.

The steps in isolation are as follows:

(1) The chamber is sterilized and in it are placed two sets of five Petri dishes each containing a hollowed slide, one or two Petri dishes for drops of washing medium, and sufficient capillary pipettes, each contained separately in a plugged glass tube.

(2) A Petri dish is placed on the stage inside the chamber and, using the right hand, ten drops of the washing medium are placed on it, the cover of the Petri dish being slightly raised with the left hand so as to admit of the insertion of the pipette. The hollowed slides are filled with washing medium.

(3) The selected organism is drawn into a pipette outside the chamber and transferred to the first drop in the Petri dish within the chamber.

(4) Air is blown in with a new capillary pipette so as to agitate the organism, which is then transferred to the second drop and so on, until it is brought into the tenth drop in the middle of the dish. If any sign of contamination is still discernible with the microscope, the organism is taken through ten further drops. A fresh pipette is used for each drop.

(5) The organism is washed successively in five or more hollowed slides each contained in a Petri dish.

(6) It is then transferred into 10 c.c. of suitable medium.

### III. ESTIMATION OF THE AMOUNT OF GROWTH

Four methods have been used for estimating the growth in the various experiments:

(a) *Computation of the number of individuals or colonies by counting.* The Sedgwick-Rafter method, as described by Whipple (1927), was first used, the ocular micrometer differing slightly in being ruled out into twenty-five squares. According to Whipple the results obtained by this method are accurate to within 10 %. It has been extensively used by Jahn (1929, 1931, 1933), Hall (1933, 1938, 1939), Elliott (1933, 1935), Loefer (1935, 1936), Johnson (1935), etc., according to whom the probable error is within 5 % and usually well below that figure (Hall, Johnson & Loefer, 1935). In the present investigation only three out of the seven sources of error enumerated by Whipple (1927, p. 98) come into consideration, viz. errors in sampling, errors in pipetting, and errors arising from unequal distribution of the organisms on the counting cell.

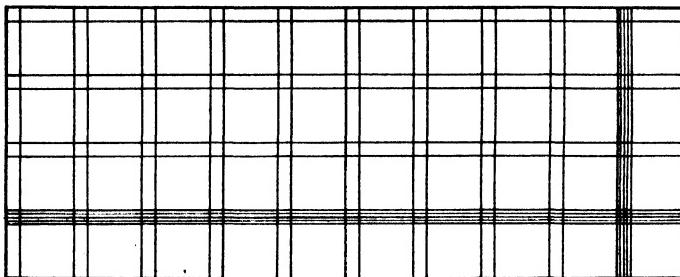


Fig. 3. Counting cell (the subdivisions of the millimetre intervals are not all shown in the figure).

Errors in sampling, according to Whipple, 'arise chiefly from the fact that organisms vary in specific gravity and in their behaviour toward light'. Since the organisms here studied are non-motile, a directive effect of light does not come into play. The amount taken up by the graduated pipette is exactly 1 c.c. and, since the quantity is further checked by the capacity of the cell (1 c.c.), errors in pipetting must be very small. After being in use for some time the capacity of the counting cell slightly increases owing to corrosion of the brass rim, but this is readily detected by the fact that the sample does not completely fill the cell and can be corrected by cleaning the rim. The chief source of error is therefore due to the unequal distribution of the material in the cell, but this is not as serious as in the mixed material used by Whipple, and can be reduced to a minimum by well shaking the sample before it is pipetted into the counting cell so that the organisms are evenly distributed.

A modification of this method was later adopted, which dispensed with the necessity of adjusting the tube length and of employing a particular combination of ocular and objective. The sample was placed in a counting cell (Fig. 3), consisting of a  $7.6 \times 3.8$  cm.

glass slide ruled into squares of 1 and 16 sq. mm. area by lines alternately 1 and 4 mm. apart; to this was cemented a brass rim (internal dimensions  $20 \times 50$  mm.) of such a thickness that the effective depth to a cover-glass placed on the top was exactly 1 mm. One c.c. of culture exactly fills the cell up to the cover-glass. A smaller size of the counting cell with a capacity of 0.5 c.c. was also used, the effective depth of this being 0.5 mm. Between the ruled lines at 1 mm. intervals three or four further ones are made to help in the counting of dense samples. Thus the organisms in units of 1, 4, 5, 16, 20, 50 or more sq.mm. can be counted without using an ocular micrometer. The number of areas counted depends on the density of the population, its evenness of distribution and the degree of accuracy required, and is readily decided after a little experience. For example, to obtain a standard error of less than 5 % with a culture of *Nitzschia palea* having more than 100,000 cells per c.c., no more than 10 random sq.mm. need be counted, while for cultures containing not more than 1000 cells per c.c. one or more counts of the whole cell are often necessary.

Table 1

No. counted	Means of 10 counts	Means of 8 counts	Means of 5 counts	No. counted	Means of 10 counts	Means of 8 counts	Means of 5 counts
180				210			
225				225			
175				190			
200				184			
190			194	230			207.8
195				195			
220				185			
230		201.875		205			
215				200			
225	205.5		217	195	201.9		196
175				205			
205				195		201.25	
210				180			
196				190			
195			196.2	210			196
206		203.375		235			
254				205			
190				205			
195				224			
220	204.6		213	215	206.4	208	216.8
Mean of 40 counts				204.6			
Standard deviation					1.94	. 3.42	16.37
Standard error					0.095 %	1.67 %	8.0 %
Probable error					0.064 %	1.13 %	5.4 %

In Table 1 are given in the order in which they were obtained the numbers of cells of *Nitzschia palea* found by counting 40 random sq.mm. in the counting cell with a capacity of 0.5 c.c.; 1 sq.mm. thus equals 0.5 cu.mm. of culture. If we take the mean of the counts of 40 random sq.mm. as the real value for 0.5 cu.mm. of the culture, the standard deviation of the mean of the counts of 10 random sq.mm. is less than 0.1 %, and that of 8 sq.mm. less than 2 %, while that of 5 random sq.mm. is still well within 10 %. It is evident that, in such a culture with 409,200 *Nitzschia* cells per c.c., counting 10 or 8 random sq.mm. gives a highly accurate estimate of the growth, and, if only a degree of accuracy with a standard error within 10 % is required, only 5 random sq.mm. need be counted.

For less dense cultures a unit of larger area than 1 sq.mm. was adopted. Table 2 gives the numbers for six samples from the same culture of *Pediastrum*, nine units, each consisting of a vertical column of the ruled cell with an area of  $1 \times 20$  sq.mm., being counted

for each sample. The standard error of the means of nine counts for each of the six samples is 1.4 %, that of the means of three units for each sample 3.8 %, and that of the counts of only one unit 6.9 %. Thus, for this culture with 15,650 colonies per c.c., counting three units will give sufficient accuracy when a standard error within 5 % is permissible, and counting only one unit is sufficient to give a standard error of less than 10 %. But, if the counting is used as a step in the estimation of surface area, more than three units must be counted so as to reduce the standard error still further.

Thus, as shown by the two instances just discussed, any required degree of accuracy can be obtained by varying the size and number of the units to be counted. Another advantage of this modification is that there is no risk of duplicating the count on the

Table 2

No. counted	Means of 3 units	Means of samples	No. counted	Means of 3 units	Means of samples
143			156		
144			148		
172	153		160	154.6	
200			149		
140			160		
170	170		152	153.6	
143			156		
150			150		
160	151	158	155	153.6	154
143			160		
145			135		
170	152.6		151	148.3	
168			160		
150			155		
160	159.3		170	161.6	
148			161		
150			160		
152	150	154	152	157.6	156
165			141		
155			155		
152	157.3		150	148.6	
157			170		
156			155		
163	158.6		155	160	
153			170		
152			165		
169	158	158	170	168.3	159
Mean of the whole series				156.5	
Standard deviation 10.8 for single units				5.93	2.17
Standard error	6.9 %	"		3.8 %	1.4 %
Probable error	4.65 %	"		2.56 %	0.94 %

same area, as might happen with the older method when a large quantity of the sample has to be counted.

For colonial forms like *Fragilaria*, *Tabellaria* and for *Oscillatoria*, with filaments of varying length, the number of cells are counted and larger quantities must be estimated; this is necessary, not only because of the variable number of cells in the threads, but also because they are less evenly distributed. The number of cells in a filament, if the latter be not too long, is readily estimated from the size of the individual cell in proportion to the total length of the filament. With *Asterionella* either the number of cells or of stars is counted, the number of cells in the latter case being computed from the average number of cells per star.

At least two samples from each culture were counted and each sample was counted at

least twice. For filamentous forms the counting was repeated three times and three samples were counted from each culture. The average of the duplicate counts was used.

(b) *Measurement of surface area.* In colonial forms like *Pediastrum* the average size of the colonies often differs in different media, so that the number of colonies alone does not give a true picture of the relative amounts of growth. As the coenobia of *Pediastrum* are generally flat plates, the volume is approximately equal to the surface area multiplied by the thickness. Since the latter varies only little as compared with the surface area, the total volume of the coenobia is in general approximately proportional to the total surface area. In certain cultures with high and unfavourable concentrations of N or P this generalization ceases to be true and the estimates for these may not be as accurate as those for lower concentrations, but they have not been used in drawing conclusions which are fundamental.

Table 3. *Growth of Pediastrum in Exp. 19 (series B), 16 days after inoculation, as estimated by different methods*

No. of culture	Conc. of NH <sub>4</sub> Cl (p.p.m.)	No. of colonies per c.c.	Average area of the colony μ <sup>2</sup>	Total area per c.c. × 10 <sup>6</sup> μ <sup>2</sup>
4	5	2460	1525	42.8
5	10	3020	1750	52.8
6	25	3000	1776	53.2
7	50	1260	3880	52.0

Table 4. *Computation of the surface area of Pediastrum coenobia in culture 5, series B of Exp. 19*

D	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	Sum
D <sup>2</sup>	4	6.25	9	12.25	16	20.25	25	30.25	36	42.25	49	—	64	—
f	1	2	16	10	8	1	6	8	7	2	1	—	1	63
fD <sup>2</sup>	4	12.5	144	122.5	128	20.25	150	242	252	84.5	49	—	64	1272.75

$$\bar{D}^2 \text{ (Average of } D^2) = \frac{S(fD^2)}{Sf} = \frac{1272.75}{63} = 20.2$$

$$A \text{ (Average area)} = \frac{S(fD^2)}{Sf} \times \frac{m^2\pi}{4} = 20.2 \times 86.6\mu^2 \left( m = 10.5\mu, \frac{m^2\pi}{4} = 86.6\mu^2 \right)$$

$$n = 3020; \therefore \text{total area per c.c.} = \frac{nS(fD^2)}{Sf} \times \frac{m^2\pi}{4} = 3020 \times 20.2 \times 86.6\mu^2 = 52.8 \times 10^6 \mu^2$$

That the total area of the colonies gives a more accurate estimate of the relative amounts of growth in different media is very obvious. For example, the number of colonies in culture 7 of Exp. 19 (Table 3) at the end of 16 days is approximately half that in culture 4 and less than half that in 5 and 6, while the total area per c.c. is larger than in 4 and about the same as in 5 and 6. Naked-eye inspection showed no notable difference in the density of cultures 5–7, while the growth in 4 was evidently inferior, this still being so at the end of 22 days when turbidity measurements were made. The results of these measurements correspond with the total areas, but not with the total number of colonies per c.c.

In estimating the width of the colony of *Pediastrum* the actual length measured was the diameter of an imaginary circle circumscribed around the periphery of the colony in such a way that the areas of the peripheral notches inside the circle were equal to the areas of the processes lying outside it. Since most of the coenobia are circular, the surface area can be taken to be  $(\frac{1}{2}D)^2 \pi$ , where  $D$  is the estimated diameter of the coenobium. For elliptical coenobia the mean value of the long and the short axes was taken as the diameter of the coenobium.

The coenobia were grouped into classes differing in diameter by half a division of the ocular micrometer, as shown in Table 4; for example, those with diameters from 3.26 to 3.75 divisions inclusive were grouped in the 3.5 class, those with diameters from 3.76 to 4.25 divisions inclusive were grouped into the 4 class and so on. The value of  $D^2$  was calculated for each coenobium measured, and the average ( $\bar{D}^2$ ) for all coenobia was calculated from the formula  $\frac{S(fD^2)}{Sf}$ , where  $f$  is the frequency and  $S$  indicates the sum (Snedecor, 1937, p. 386). The total area per unit volume of culture is then  $\frac{nS(fD^2)\pi}{Sf \cdot 4}$ , where  $n$  is the total number of coenobia.

For convenience the total area of a culture was computed as in Table 4 from the formula  $\frac{nS(fD^2)}{Sf} \times \frac{m^2\pi}{4}$ , where  $D$  is the diameter of the coenobium expressed in divisions of the ocular micrometer, and  $m$  is the equivalent of one division in  $\mu$ .

The diameter measurements were always repeated with a second sample from the same culture. If the two averages differed from the mean by more than 2 %, another two samples were measured, the mean of the four averages being used as the average diameter of the colonies in the culture.

There are two main sources of error in the estimation of the total area per unit volume, viz. (1) in the counting of the number of colonies (see p. 289) and (2) in the measurement of their diameters. Since the total error is increased by the second of these, a higher degree of accuracy is required in counting than for unicellular organisms, such as *Nitzschia*. Since the surface area of the coenobium is calculated from the square of the diameter, any error in the estimation of the latter is increased so that the second source of error is very important.

Table 5 gives the diameter measurements of eighty coenobia from each of three parallel cultures made under similar conditions, as well as the means and standard errors when different numbers of coenobia were measured. The data show that the main source of error is not due to the difference in mean coenobium diameter in the different cultures, since the mean of the diameter measurements for any culture is well within 0.5 % of the mean for the three cultures. The accuracy is greatly increased by increasing the number of coenobia measured. Thus, if only ten coenobia be measured, the standard error is 9.5 %, but if twenty, forty or sixty be measured the standard error decreases to 5.3, 2.3 and 1.9 % respectively.

The standard error of the area means in the above example was 4.6 % when forty coenobia were measured (diameter error 2.3 %) and 2.8 % when sixty coenobia were measured (diameter error 1.9 %). The number of colonies measured in the present investigation was never less than sixty, the standard diameter error never being allowed to exceed 2 %; and hence the standard error for the average area estimates was always within 4 %. Thus, with a standard counting error of less than 3 %, the degree of accuracy of area estimates is still high, the standard error not exceeding 7 %.

The colonies measured must not be selected at random, since there is apt to be an unconscious tendency to choose a disproportionately large number of colonies of a certain size. Every colony inside a unit area of the counting cell must therefore be measured. Even distribution of the sample is also important. The sample should be pipetted out immediately from the middle of the carefully shaken culture. A suitable concentration of

the sample obtained by centrifuging or diluting is also needed, so that the colonies do not overlap or are not too widely spaced.

(c) *Estimation of dry weight.* The minute quantity of growth obtained in the cultures does not justify the use of this method unless a microbalance with a high degree of sensitivity is available. For the limited use of such a balance the writer is indebted to the Nutritional Laboratory of the University of Cambridge. The instrument used was Kuhlmann's no. 19B, its sensitivity being 0.001 mg. With this the growth in cultures with 50 c.c. of medium could be estimated. Difficulties were experienced at the beginning in

Table 5. *Diameter measurements of the colonies from three parallel cultures, in terms of divisions of the ocular micrometer (one division = 10.5 $\mu$ )*

												Means of			
												10	20	40	60
<b>Culture 1. Average diameter = 3.64375</b>															
4.5	2.5	2.5	4.0	2.0	2.0	4.0	4.0	2.5	3.0	3.10	—	—	—	—	—
3.0	4.5	3.0	7.5	3.0	2.5	3.0	3.5	2.0	4.0	3.60	3.350	—	—	—	—
5.0	5.5	3.0	2.5	2.5	3.5	2.5	4.5	4.5	4.0	3.75	—	—	—	—	—
3.5	3.0	2.5	7.5	2.5	5.5	5.5	4.0	3.0	2.5	3.95	3.850	3.6000	—	—	—
3.0	2.0	2.5	4.5	6.0	2.5	3.0	2.5	2.0	2.5	3.05	—	—	—	—	—
3.5	4.5	3.0	3.5	5.5	4.5	2.5	4.0	4.0	4.0	4.00	3.525	—	—	3.575	—
3.5	4.0	3.5	5.5	5.5	2.0	2.5	2.5	2.5	3.0	3.45	—	—	—	—	—
4.5	2.5	2.5	4.5	5.0	7.0	2.5	3.0	5.5	5.5	4.25	3.850	3.6785	—	—	—
<b>Culture 2. Average diameter = 3.6345</b>															
3.5	3.0	2.0	2.5	7.5	2.5	3.0	4.5	3.0	5.0	3.65	—	—	—	—	—
4.5	3.0	2.5	2.5	2.5	4.5	2.5	4.0	4.5	2.0	3.25	3.450	—	—	—	—
2.5	3.5	4.0	3.5	5.0	5.5	2.0	3.5	4.5	2.5	3.65	—	—	—	—	—
3.0	3.0	3.5	5.0	4.5	4.0	2.0	3.0	4.5	3.0	3.55	3.600	3.5250	3.633	—	—
3.0	4.5	2.5	2.0	5.5	3.0	2.5	2.5	2.0	5.5	3.25	—	—	—	—	—
6.0	4.5	3.0	3.0	2.0	4.5	5.5	4.0	3.5	3.0	3.85	3.550	—	—	—	—
3.5	3.0	3.0	4.5	2.5	3.0	3.5	4.5	3.0	8.0	3.85	—	—	—	—	—
3.0	3.5	4.0	3.0	5.0	3.5	5.5	4.0	6.5	2.5	4.05	3.950	3.7500	—	—	—
<b>Culture 3. Average diameter = 3.65</b>															
2.5	2.0	2.5	2.5	3.0	3.5	3.0	6.0	2.0	2.5	3.05	—	—	—	—	—
4.5	3.5	2.5	3.0	4.5	5.0	3.0	3.5	5.5	4.5	3.95	3.500	—	—	3.668	—
2.5	3.5	4.5	4.5	6.0	3.5	4.5	5.0	3.5	2.0	3.95	—	—	—	—	—
2.5	5.5	2.5	2.5	3.0	4.5	4.5	2.5	3.0	4.0	3.45	3.700	3.6000	—	—	—
3.0	4.5	4.5	3.5	2.5	2.5	2.5	3.5	3.0	3.0	3.25	—	—	—	—	—
3.0	3.0	2.5	4.5	5.0	7.0	3.0	3.0	2.5	4.5	3.85	3.550	—	—	—	—
5.0	4.5	4.5	2.5	2.0	3.0	4.0	2.5	6.0	4.0	3.90	—	—	—	—	—
4.5	4.0	2.0	2.5	3.5	5.0	7.5	2.0	2.5	4.5	3.80	3.850	3.7000	3.700	—	—
												0.344	0.182	0.0828	0.0689
												9.5 %	5.3 %	2.3 %	1.9 %
												6.4 %	3.6 %	1.5 %	1.3 %
												4.6 %	2.8 %	—	—
												3.1 %	1.9 %	—	—

finding a suitable container for the material during drying and weighing. Various kinds of filter paper proved to be useless and even small glass vials were found to absorb moisture after drying at 100° C. during the period of weighing. Finally, small containers made of aluminium foil, about 25 $\mu$  thick and weighing between 320.4 and 330.026 mg., proved satisfactory.

The sample was washed five times successively with distilled water by centrifuging, in order to ensure complete sedimentation. The speed and duration of centrifuging varied for each organism. The estimated material is transferred to a numbered and previously weighed container. The centrifuge tube is rinsed five times in succession with 1 c.c. of distilled water to ensure removal of all the material. The containers with the material

are dried in an electric oven at 100° C., the drying being continued for 5 hr. after all liquid has disappeared. The containers are then folded with forceps and placed in a desiccator to cool before weighing.

Dry-weight determinations are more reliable in cultures with larger amounts of growth. In others (e.g. cultures 1-3 of Exp. 18, series A) the weight determined is often in excess of the correct value, probably owing to insoluble precipitates which are not washed out. For more vigorous cultures the dry-weight estimations correspond well (cf. Fig. 4) with those of total area and turbidity. Objections to this method are the time required and the care necessary to ensure proper sampling, washing, drying and weighing.

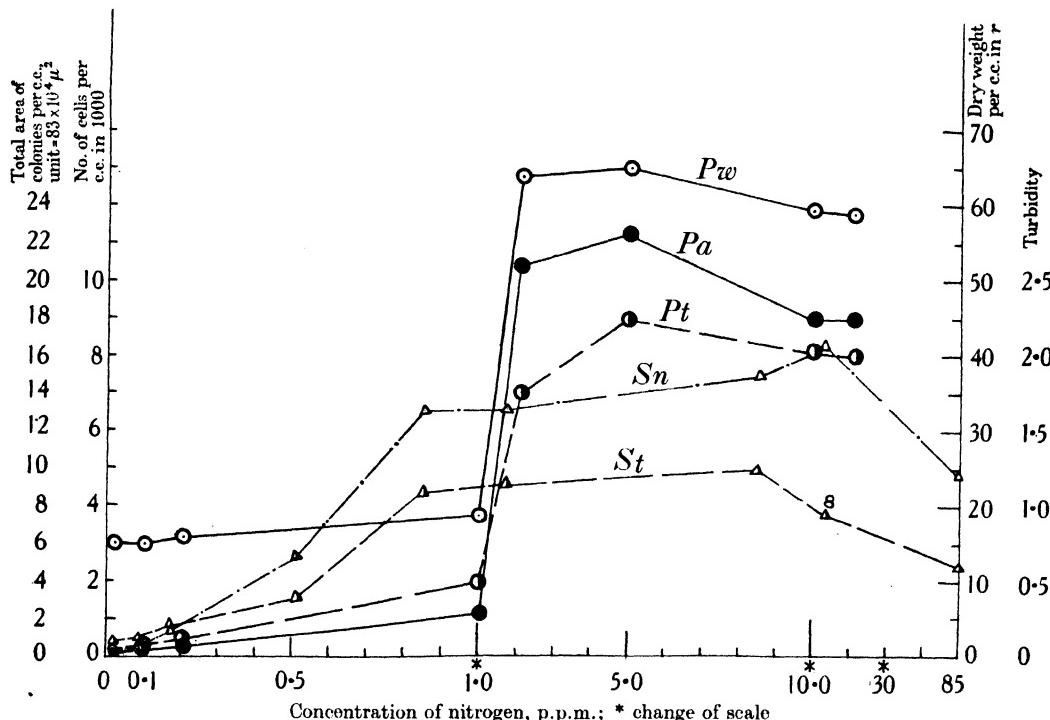


Fig. 4. Estimation of growth of *Staurastrum* (St and Sn) and *Pediastrum* (Pt, Pa and Pw) by different methods: St, turbidity, and Sn, number of *Staurastrum*-cells (Exp. 22, 32 days); Pt, turbidity, Pa, area, and Pw, dry weight of *Pediastrum* (Exp. 18, series A, 12 days).

(d) *Turbidity measurements.* Turbidity, as estimated by the length of liquid columns possessing equal turbidity or by comparison with standard suspensions, has long been used as a method for determining the concentration of suspensions of yeast and bacteria (Richard & Wells, 1905; McFarland, 1907; Peskett, 1927). One defect of the original method lies in the unavoidable personal element. Williams, McAlister & Roehm (1929) introduced an improvement consisting in the measurement of the galvanometric deflexion produced by a specially prepared thermocouple, the suspension being placed between the latter and the source of light. The Metropolitan Water Board (1936, p. 30) have devised an apparatus for estimating the turbidity of water in which a photoelectric cell is used, and a modification of this has proved very satisfactory and has been used extensively in the present work.

The apparatus (Fig. 4) consists of a rectangular wooden case, painted dull black inside and serving as a totally enclosed optical bench, along the axis of which are placed in sequence a source of light (*C*), a condensing lens system (*D*<sub>1</sub>*D*<sub>2</sub>), an adjustable iris diaphragm (*E*), a water tank (*W*), and a photoelectric cell (*H*). The source of light is an 8 V. electric lamp fed from four 2 V. accumulators and controlled by a switch (*A*) outside the case. The condensing lenses (*D*<sub>1</sub>*D*<sub>2</sub>) are mounted in a sliding tube, allowing the light to be focused on the slit (*w*<sub>1</sub>). The intensity of illumination on the photoelectric cell, and therefore the deflexion of the microammeter to which this is connected, can be adjusted by the variable diaphragm (*E*) controlled from outside the case by the milled head (*I*). The purpose of the parallel-sided glass water tank (*W*) is to eliminate the irregular reflexion and refraction at the sides of the culture tube. This, during an estimation, is placed in the water and is located centrally by a circular depression (*L*) in the bottom of the tank and a corresponding hole in the top of the case, through which the culture tube may be

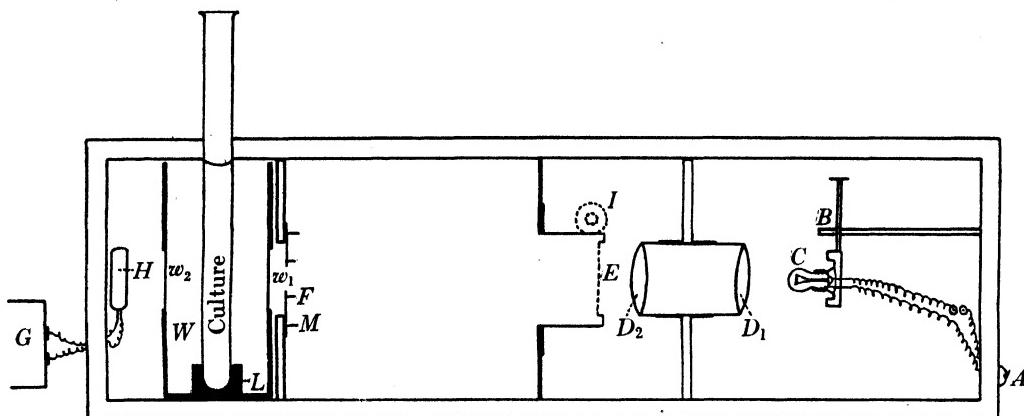


Fig. 5. Elevation of the photo-electric nephelometer for measuring the density of cultures.

placed in position without opening the apparatus. On the two surfaces of the water tank through which the light passes are black paper screens, each having a narrow slit (*w*<sub>1</sub>, *w*<sub>2</sub>), 32 × 5 mm., to restrict the pencil of light to the centre of the culture tube. The photoelectric cell is a Weston, Model 594, and is used in conjunction with a microammeter supplied by the Cambridge Instrument Co. giving 75 mm. deflexion for 24 $\mu$ A. A provision (*M*) acting as a holder for large flat-bottomed culture tubes and another (*F*) for small ones allows the apparatus to be used in a vertical position if desired, the water tank then of course being removed since it is not required. The provision (*F*) is removed when the culture is measured in large flat-bottomed tubes.

To obtain a reading the iris diaphragm (*E*) is first adjusted so that the deflexion is 20 $\mu$ A. when no culture tube is inserted. This must be the same for all the cultures of a given experiment. When a tube containing tap water or a medium without algal growth is introduced, the deflexion is 19·4–19·8, so that the decrease due to the tube is only 0·2–0·6 $\mu$ A. An estimation occupies about a minute. The voltage of the accumulators can be kept fairly constant by keeping them on continuous trickle charge from the mains while readings are being taken, so that as a general rule little or no adjustment of the iris diaphragm is needed during the estimation of a series of ten or more cultures. The degree

of turbidity of a culture is shown by the decrease in the amount of deflexion of the microammeter, and is taken as the ratio of the decrease in deflexion to the original deflexion. Since, however, the original deflexion was always  $20\mu A$ . (by adjustment), only the actual decrease in deflexion has been recorded and is here used throughout as a measure of the turbidity. Strictly speaking, the difference in deflexion should not be taken as directly proportional to the density of the suspension, since the relation is not a linear but an exponential one. Since, however, the suspensions estimated by this method were not very dense and with very weak suspensions the relation becomes nearly linear, this measure was considered sufficiently accurate for the present purposes. When the culture is removed from the water tank, the microammeter pointer should return to its previous position; if it does not, there must have been a change in the voltage of the accumulators and the diaphragm must be readjustable and a fresh estimation made. After each series of estimations the water in the tank is changed, since it often becomes slightly turbid.

The method of estimation by turbidity is more useful than the other methods when the size of the individual organisms varies to any appreciable extent. When the individuals or colonies in a certain culture are smaller than in other cultures of the same experiment, estimation by number of cells or colonies per unit volume often gives an exaggerated idea of the growth (cf. Fig. 4, curves *St* and *Sn*, culture 8). On the other hand, when individuals or colonies are larger, estimation by number or total area tends to give too small an estimate of the growth. Turbidity, however, is not only a function of the number of individuals or colonies, but also of the size and the density of the cell contents. Turbidity measurements of *Pediastrum* take also into account the thickness of the colonies, which is ignored in estimations of aggregate area.

A further advantage of this method lies in the fact that the growth of cultures can be estimated at frequent intervals without removing samples from the culture tubes. At the end of an experiment the final growth can be estimated in the following way. The water tank (*W*) is removed and the turbidity apparatus placed in an upright position. For estimation the well-shaken material is poured into a cylindrical flat-bottomed tube with a capacity of only 8 c.c. Such a tube can be used for small cultures (e.g. 10 c.c.) as well as larger ones. It is fixed into the socket *F* and covered with a cover-glass during the estimation. A 40 c.c. estimation tube was also used sometimes when all the cultures of one experiment were started with 50 c.c. of media, when socket *M* was used after the removal of socket *F*.

The method of turbidity measurement is not only quick but also gives perfectly constant results. Readings with the same culture or with cultures showing equal growth are always precisely the same. Its accuracy is shown by the high degree of correspondence between the results obtained in this way and those obtained by counting or area estimation or by dry-weight determinations (see Figs. 4 and 7). In view of this correspondence, the number of cells in a culture or the total area of colonies (as in *Pediastrum*) can be approximately judged by constructing a nomogram with as much accuracy as by actual counting and area estimation.

In applying this method it is necessary that the culture is well shaken and evenly distributed. Filamentous organisms, like *Fragilaria* or *Tabellaria* or those which tend to become clustered, require prolonged shaking in order to break the filaments or clusters into smaller fragments. To avoid errors due to inequalities in the tubes, these must have uniform inside and outside diameters in the different cultures of an experiment. There is

often a noticeable difference in the amount of light cut off by the different sides of a test-tube. After insertion in the apparatus the tube should be rotated until the position in which the least light is cut off is found. The smallest difference between the deflexions of the microammeter before and after the culture is introduced is taken as the correct reading. The large tubes used in the later experiments are preferable to small ones, since the thickness of the glass is more uniform and the refraction due to curvature of the surface much smaller. The reduction of deflexion caused by the test-tube alone, which is estimated before the culture is started, is subtracted from the actual readings.

#### IV. SUITABLE CULTURE SOLUTIONS FOR VARIOUS PLANKTONIC ALGAE

The following culture solutions have been used in the present investigation, the amounts always being in grams per litre of Pyrex glass-distilled water.

1		7 ( <i>Staurastrum</i> )
$\text{NH}_4\text{NO}_3$	0.025	$\text{Ca}(\text{NO}_3)_2$ 0.03
$\text{K}_2\text{HPO}_4$	0.001	$\text{K}_2\text{HPO}_4$ 0.005
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.025	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.07
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	0.025	$\text{K}_2\text{SiO}_3$ 0.02
$\text{FeCl}_3$	0.0005	$\text{Na}_2\text{CO}_3$ 0.03
2 ( <i>Botryococcus</i> )		$\text{FeCl}_3$ 0.001
$\text{KNO}_3$	0.025	8 ( <i>Pediastrum</i> )
$\text{K}_2\text{HPO}_4$	0.001	$\text{KNO}_3$ 0.025
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.025	$\text{K}_2\text{HPO}_4$ 0.001
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	0.025	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.025
$\text{FeCl}_3$	0.0005	$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$ 0.001
3		$\text{K}_2\text{CO}_3$ 0.005 (or up to 0.05)
$(\text{NH}_4)_2\text{SO}_4$	0.025	$\text{FeCl}_3$ 0.0008
$\text{K}_2\text{HPO}_4$	0.001	9 ( <i>Asterionella</i> , <i>Nitzschia</i> , <i>Tabellaria</i> )
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.025	$\text{Ca}(\text{NO}_3)_2$ 0.02-0.04
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	0.025	$\text{K}_2\text{HPO}_4$ 0.002
$\text{FeCl}_3$	0.0005	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.01
4		$\text{K}_2\text{SiO}_3$ 0.025
$(\text{NH}_4)_2\text{HPO}_4$	0.025	$\text{CaCO}_3$ 0.01
$\text{K}_2\text{HPO}_4$	0.001	$\text{FeCl}_3$ 0.001
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.025	10 ( <i>Botryococcus</i> , <i>Staurastrum</i> , <i>Oscillatoria</i> , <i>Asterionella</i> , <i>Tabellaria</i> , <i>Nitzschia</i> )
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	0.025	$\text{Ca}(\text{NO}_3)_2$ 0.04
$\text{FeCl}_3$	0.0005	$\text{K}_2\text{HPO}_4$ 0.01 or 0.005
5 ( <i>Pediastrum</i> )		$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.025
$(\text{NH}_4)_2\text{SO}_4$	0.025	$\text{Na}_2\text{CO}_3$ 0.02
$\text{K}_2\text{HPO}_4$	0.005	$\text{Na}_2\text{SiO}_3$ 0.025
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.07	$\text{FeCl}_3$ 0.0008
$\text{NaCl}$	0.04	11 ( <i>Staurastrum</i> , <i>Pediastrum</i> )
$\text{K}_2\text{SiO}_3$	0.02	$\text{KNO}_3$ 0.04
$\text{CaCO}_3$	0.01	$\text{K}_2\text{HPO}_4$ 0.001
$\text{FeCl}_3$	0.001	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.025
6 ( <i>Pediastrum</i> )		$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$ 0.001
$\text{NH}_4\text{Cl}$	0.025	$\text{K}_2\text{CO}_3$ 0.05
$\text{K}_2\text{HPO}_4$	0.005	$\text{K}_2\text{SiO}_3$ 0.01
$\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$	0.06	$\text{FeCl}_3$ 0.001
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.07	
$\text{K}_2\text{SiO}_3$	0.02	
$\text{CaCO}_3$	0.01	
$\text{FeCl}_3$	0.001	

12		CaCO <sub>3</sub>	0.01
( <i>Botryococcus</i> , <i>Staurastrum</i> , <i>Asterionella</i> , <i>Tabellaria</i> , <i>Nitzschia</i> )		NaHCO <sub>3</sub>	0.04
Ca(NO <sub>3</sub> ) <sub>2</sub>	0.03	FeCl <sub>3</sub>	0.001
K <sub>2</sub> HPO <sub>4</sub>	0.005		
MgSO <sub>4</sub> .7H <sub>2</sub> O	0.075	Solution 14 with Ca(NO <sub>3</sub> ) <sub>2</sub> replaced by (NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub>	
K <sub>2</sub> SiO <sub>3</sub>	0.025		15
KCl	0.005		16
Na <sub>2</sub> CO <sub>3</sub>	0.02	( <i>Fragilaria</i> , <i>Nitzschia</i> )	
FeCl <sub>3</sub>	0.0005	Ca(NO <sub>3</sub> ) <sub>2</sub>	0.05
13		K <sub>2</sub> HPO <sub>4</sub>	0.001
( <i>Botryococcus</i> )		MgSO <sub>4</sub> .7H <sub>2</sub> O	0.04
KNO <sub>3</sub>	0.05	K <sub>2</sub> SiO <sub>3</sub>	0.025
K <sub>2</sub> HPO <sub>4</sub>	0.01	CaCl <sub>2</sub> .6H <sub>2</sub> O	0.04
MgSO <sub>4</sub> .7H <sub>2</sub> O	0.025	Na <sub>2</sub> CO <sub>3</sub>	0.02
CaCl <sub>2</sub> .6H <sub>2</sub> O	0.02	FeCl <sub>3</sub>	0.001
FeCl <sub>3</sub>	0.001		17
14			( <i>Asterionella</i> )
( <i>Nitzschia</i> )		NH <sub>4</sub> Cl	0.02
Ca(NO <sub>3</sub> ) <sub>2</sub>	0.02-0.04	K <sub>2</sub> HPO <sub>4</sub>	0.001
K <sub>2</sub> HPO <sub>4</sub>	0.002	MgSO <sub>4</sub> .7H <sub>2</sub> O	0.04
MgSO <sub>4</sub> .7H <sub>2</sub> O	0.04	K <sub>2</sub> SiO <sub>3</sub>	0.025
NaCl	0.04	CaCl <sub>2</sub> .6H <sub>2</sub> O	0.04
K <sub>2</sub> SiO <sub>3</sub>	0.025	Na <sub>2</sub> CO <sub>3</sub>	0.02
		FeCl <sub>3</sub>	0.001
<i>Micrometabolic elements solution</i>			
ZnSO <sub>4</sub> .7H <sub>2</sub> O	0.002	H <sub>3</sub> BO <sub>3</sub>	0.002
MnSO <sub>4</sub> .4H <sub>2</sub> O	0.002	LiCl	0.001
Na <sub>2</sub> SiO <sub>3</sub>	0.002	CoCl <sub>2</sub> .6H <sub>2</sub> O	0.001
AlCl <sub>3</sub>	0.002		

### 1. *Pediastrum boryanum* (Turp.) Menegh.

Exp. 1. The material, obtained from an artificial pond in a London garden, contained *Pediastrum Boryanum* as the dominant organism; apart from this, there were also present *Scenedesmus*, *Closterium*, *Trachelomonas*, *Nitzschia* and occasional filaments of *Fragilaria* and *Mougeotia*. In the preliminary experiments the various media (A-G) enumerated in Table 6 were tested. One series (I) of cultures was placed in a cool greenhouse without artificial light, while another series (II) was exposed in apparatus A (p. 285) and illuminated by four 60 W. lamps throughout the 24 hr. 50 c.c. of each medium, contained in a 250 c.c. Pyrex conical flask, was inoculated with 20 drops of the material. After 13 days the two series afforded the results shown in Table 6. They show that the growth of *Pediastrum* is favoured by longer illumination. In series I there was no growth in solutions B, C, E, F, although there was slight growth in these solutions under continuous light. In Benecke's solution, with or without soil extract (A and D), *Pediastrum* grows better in the continuously illuminated cultures. This solution is more suitable for *Pediastrum* than Bristol's or Czurda's. The former is probably defective owing to the high concentration of N, P, Ca, Mg and Na, while Czurda's mainly fails owing to the high Ca concentration, since a later experiment (6) shows that Ca has a definite inhibiting effect in these concentrations. *Pediastrum* grows better in the diverse solutions with soil extract than without. Other solutions (Knop, Kufferath, Petersen, Pringsheim (1926), Conrad, Molisch, Pfeffer (cf. Kufferath, 1929) and De (1939)) were tried later, but no better growth was obtained than that in Benecke's solution, either in natural daylight

or under artificial illumination. Since my aim was to find a solution suitable for growing *Pediastrum* in large quantities, no further investigations were made with mixed cultures, where the factors influencing the growth of one organism are complicated by the presence of others.

Pure cultures of *Pediastrum* were raised on agar plates prepared with 1·5% agar powder in Benecke's solution containing 5% soil extract. A single colony within 3 weeks gives rise to a considerable aggregate on the plate. From such growths inoculations were made into 100 c.c. Benecke's solution with 5% soil extract. One set (A) of these cultures was placed under artificial light at a temperature of  $22 \pm 2^\circ \text{C}$ ., another set (B) inside the cold apparatus B ( $9 \pm 1^\circ \text{C}$ .). In both sets the cultures within a fortnight included equally plentiful *Pediastrum* colonies, so that temperature does not seem to have much effect, at least within the range  $8\text{--}24^\circ \text{C}$ . and is certainly far less significant than light.

Table 6. Growth of *Pediastrum* in diverse culture solutions

Culture solutions	A	B	C	D	E	F	G
<i>Pediastrum</i>	P	0	0	P	0	0	0
	P	P	P	g	g	g	0
<i>Scenedesmus</i>	0	0	p	p	0	p	0
	g	0	P	g	0	g	0
<i>Trachelomonas</i>	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
<i>Closterium</i>	P	0	0	g	0	0	0
	P	0	0	g	0	0	0
<i>Nitzschia</i>	P	P	P	g	g	g	0
	P	P	P	g	g	g	0
<i>Fragilaria</i>	0	0	0	0	0	0	0
	P	0	0	P	0	P	0
<i>Mougeotia</i>	0	0	0	P	0	0	0
	g	0	0	g	0	P	0

A = Benecke, B = Bristol, C = Czurda (for the formulae of solutions A-C see Kufferath, 1929), D = Benecke + 5%\* soil extract, E = Bristol + 5% soil extract, F = Czurda + 5% soil extract, G = 5% soil extract in distilled water, p = poor, g = good, 0 = no or very little growth. The upper letters refer to series I, the lower to series II.

Direct transference of an isolated colony into Benecke's solution with soil extract gave equally good results. From that time onward subcultures were made once a fortnight in this solution until a more satisfactory medium was found.

#### (a) The concentration of nitrogen in the culture solution

In most of the solutions used for the culture of algae the amount of N-containing salts is more than in Benecke's solution ( $\text{NH}_4\text{NO}_3 = 0\cdot1 \text{ g./l.}$ ). It therefore seemed probable that the low N concentration was one of the factors causing better growth in Benecke's solution than in the others. A dense growth of *Pediastrum* is often found in natural waters, where the N concentration is generally much lower than in Benecke's solution, the average nitrate ( $\text{NO}_3^-$ ) content of surface waters, according to Murray's (1887) estimation, being 4·2 p.p.m. or  $N = 0\cdot95 \text{ p.p.m. or mg./l.}$  The N content of the Illinois River, where *Pediastrum* was one of the prominent planktonts throughout the year (Kofoid, 1903), was never more than 13 p.p.m. This suggests that good growth of *Pediastrum* might be obtained

\* The soil extract was always prepared by autoclaving for half an hour at 20 lb. pressure 1 kg. of garden soil with 1 l. of tap water. After standing 4 days the clear supernatant liquid was decanted off and autoclaved. This was allowed to stand for another 4 days when the clear fluid was again decanted and autoclaved.

in N concentrations lower than that in Benecke's solution. An attempt was therefore made to determine the most suitable N concentration.

*Exp. 2.* Duplicate series of nine 100 c.c. cultures in 250 c.c. conical flasks with Benecke's solution, with  $\text{NH}_4\text{NO}_3$  varying from 0 to 500 p.p.m. ( $N=0-174$  p.p.m.) exposed in apparatus A; inoculum 18 (mostly 16-32 celled) colonies per c.c. (Fig. 6).

Fig. 6 shows the number of colonies 26 and 46 days respectively (A, B) after inoculation and the average areas (D) of the colonies in the two series as measured on the 46th day. In the absence of N there is scarcely any growth, there being only twenty-five and thirty colonies per c.c. respectively after 26 days. The best growth is at first obtained in

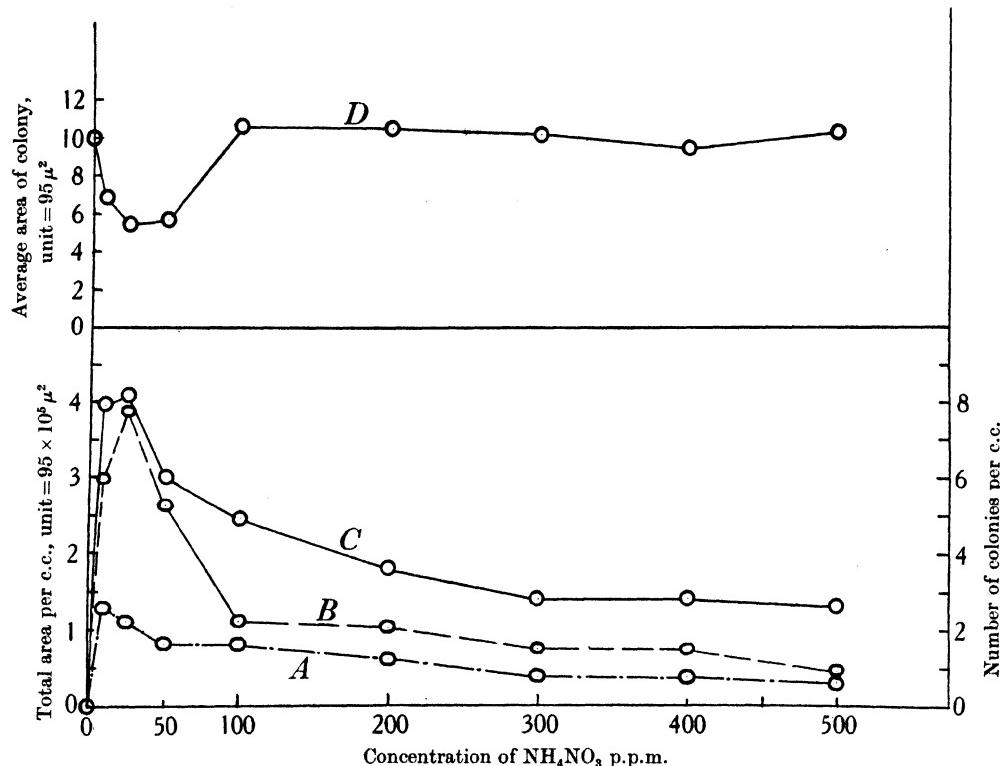


Fig. 6. Growth of *Pediasium Boryanum* in Benecke's solution with varying concentrations of  $\text{NH}_4\text{NO}_3$ : A and B, numbers of colonies, A, after 26 days, B, after 46 days; C, total area, 46 days; D, average area of colony (Exp. 2).

cultures with a  $\text{NH}_4\text{NO}_3$  concentration of 10 ( $N=3.5$ ) and 25 ( $N=8.7$ ) p.p.m. respectively. With higher concentrations there is a gradual decrease in the number of colonies, although above 200 p.p.m. the decrease is less significant. As the cultures aged, the growth in 10 p.p.m. of  $\text{NH}_4\text{NO}_3$  became inferior to that in 25 p.p.m. While there was at first not much difference in cultures with 50 p.p.m. and 100 p.p.m. of  $\text{NH}_4\text{NO}_3$ , growth was later definitely better in 50 p.p.m. This is evidently due to absorption of part of the  $\text{NH}_4\text{NO}_3$ , so that the concentration which was suitable at first becomes deficient and that which was too high approaches more and more to a suitable one in the older cultures. The experiment shows that only a tenth of the concentration of  $\text{NH}_4\text{NO}_3$  usually used in Benecke's solution is needed for optimum growth. A concentration of half that in Benecke is already

too high, and higher concentrations produce an inhibiting effect. The high N concentration is no doubt one of the reasons why the media hitherto employed do not admit of satisfactory growth of this organism.

The most suitable N concentration during the early period of the experiment is very near to the average (3.2 p.p.m.) of the sixty-six natural waters analysed by the Metropolitan Water Board (1937) which indicates that its concentration in natural waters is at about the optimum for the growth of *Pediastrum*. The maximum of *P. Boryanum* in the Illinois in 1908 corresponds to a maximum of total inorganic nitrogen (2.9 p.p.m.) which is near the optimum established in Exp. 2.

The average size of the coenobia in different cultures is in inverse relation to the rate of multiplication, as shown in Fig. 6D, where the average areas of both series on the 46th day are plotted. In higher N concentrations the cells of large coenobia often have denser contents than in the optimum concentrations.

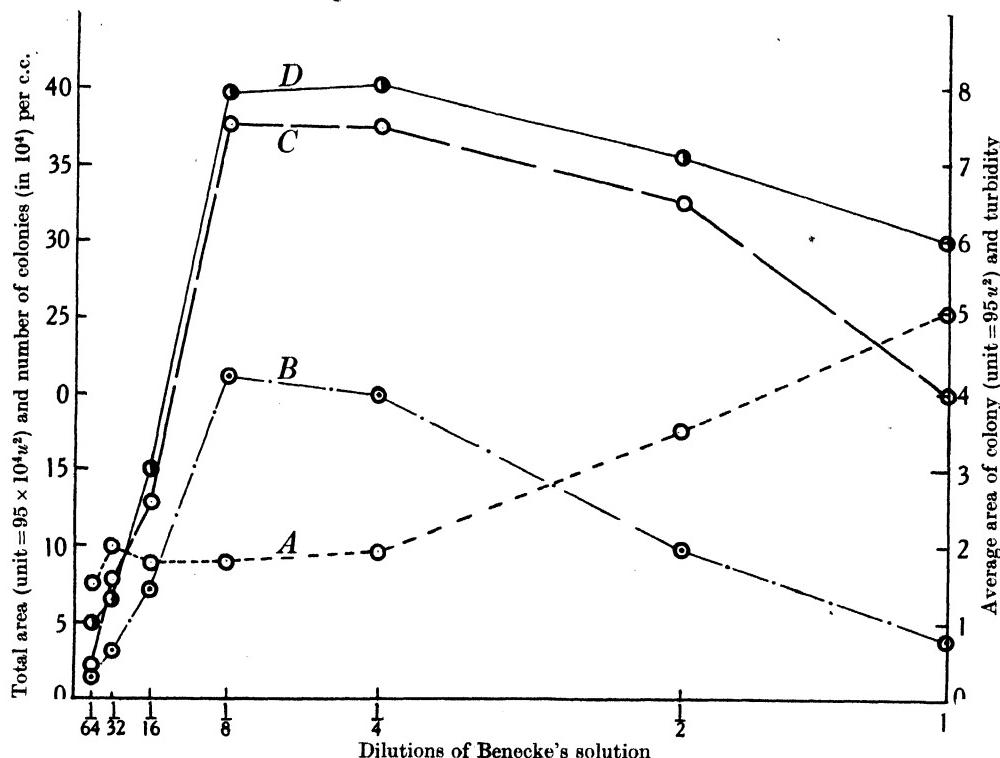


Fig. 7. Growth of *Pediastrum Boryanum* (42 days) in different dilutions of Benecke's solution (Exp. 3): A, average area of colony; B, number of colonies; C, total area; D, turbidity.

#### (b) The concentration of the culture solution

Benecke's solution, with a total solid content of 250 p.p.m., is one of the most dilute media used for culturing algae. The total mineral residue of natural fresh waters varies from less than 30 to more than 18,000 p.p.m., but is usually less than that of Benecke's solution, the average of surface waters, according to Murray's estimation, being 152 p.p.m. Exp. 2 suggests that the growth of *Pediastrum* may be favoured also by a lower concentration of other constituent salts. Different dilutions of Benecke's solution were therefore tested.

*Exp. 3.* Duplicate series of seven 10 c.c. cultures in test-tubes with different dilutions of Benecke's solution (normal, 1/2, 1/4, 1/8, 1/16, 1/32 and 1/64); inoculum, approximately 370 colonies in 10 drops from a 7-day-old subculture in Benecke's solution with 0·025 g. of  $\text{NH}_4\text{NO}_3$  per litre; 7 hr. daily exposure in apparatus A (Fig. 7).

At the beginning the best growth occurred in 1/4 and 1/8 Benecke. For the first few days it was nearly as good in 1/16 Benecke, but it soon became much inferior. That in 1/32 and 1/64 Benecke was very poor from the beginning, and the colonies gradually lost their green colour. The cultures in 1/16 Benecke also became yellowish after 7 weeks, while those in higher concentrations remained green. In the normal solution and in that of half strength the growth was always inferior to that in 1/8 and 1/4 strength, while that in the normal solution was inferior to that in 1/2 Benecke, though the difference was less and less pronounced in later periods.

In concentrations greater than 1/4 Benecke the average area of colony increases with increasing concentration (Fig. 7 A) while the rate of multiplication decreases (Fig. 7 B), a phenomenon comparable with that observed in Exp. 2. There is no striking difference in average area from 1/4 to 1/64 Benecke (Fig. 7 A). The number of colonies (B), the total area per c.c. (C), the average area (A) and turbidity measurements (D) after 42 days are shown in Fig. 7, which are based on average values of the two series.

This experiment shows that dilutions of Benecke down to 1/8 of the normal strength support better growth than the full solution, but it also suggests that the beneficial effect may be mainly due to dilution of the nitrogenous constituent. The relative amounts of growth in different cultures correspond very closely with those in Exp. 2 with about the same range of nitrogen concentration, and the two most successful cultures in these experiments occur in approximately the same nitrogen concentrations. The advantage of dilution might, however, also be due to other constituents, for instance, phosphate.

#### (c) *The concentration of phosphate*

*Exp. 4.* Cultures with three concentrations of  $\text{NH}_4\text{NO}_3$  (50, 25 and 12·5 p.p.m.) for each of five concentrations of  $\text{K}_2\text{HPO}_4$  (0·5, 1·0, 5·0, 10·0 and 25·0 p.p.m.),  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  and  $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$  each being 25 p.p.m. with a trace of  $\text{FeCl}_3$  (0·5 p.p.m.). The fifteen solutions thus have  $\text{NH}_4\text{NO}_3$  varying between that in 1/2 and that in 1/8 Benecke and  $\text{K}_2\text{HPO}_4$  approximately that of 1/2 to 1/64, while the amount of  $\text{MgSO}_4$  and  $\text{CaCl}_2$  is that in 1/2 Benecke.

For the first 2 weeks the growth in 12·5 p.p.m. of  $\text{NH}_4\text{NO}_3$  for all concentrations of  $\text{K}_2\text{HPO}_4$  was a little better than that in 25 p.p.m. and this was better than in 50 p.p.m. After 3 weeks the first two were about equal, while after 6 weeks the 25 p.p.m. afforded better growth than either of the others. This result corresponds approximately with that of Exp. 2, although the variation in P concentration is so considerable. The growth in the various concentrations of  $\text{K}_2\text{HPO}_4$  in three different concentrations of  $\text{NH}_4\text{NO}_3$  correspond with each other and the results can be briefly summarized as follows:

$$2 \text{ weeks } 1\cdot0 = 5\cdot0 > 0\cdot5 > 10 > 25$$

$$4 \text{ weeks } 1\cdot0 = 5\cdot0 > 0\cdot5 > 10 > 25$$

$$6 \text{ weeks } 1\cdot0 = 5\cdot0 = 10 > 25 > 0\cdot5$$

Even half the concentration of phosphate in Benecke's solution is therefore still too high for optimum growth of *Pediastrum* and concentrations down to 1 p.p.m. are favourable.

*Growth of planktonic algae*

Table 7. Concentrations of important mineral constituents of natural freshwaters, in p.p.m.

Source	Water	N	P	F <sub>e</sub>	Ca	Mg	K	SiO <sub>2</sub>	Total solids
Clarke, 1924	Lake Superior	0.001	—	0.0007	13	0.03	0.03 (K+Na)	0.08	0.6
Dole, 1909	Lake Superior	0.113	—	0.044	3.1	1.5	3.2 (K+Na)	7.4	60
Clarke, 1924	Byske-elf	—	—	—	2.2	0.72	1.7	1.5	19.2
Pearsall, 1930, 1922	Ennerdale	0.016	—	0.01	—	—	5.8 (K+Na)	1.0	30.9
—	—	0.009	—	0.05	10	—	—	2.2	—
Pearsall, 1930, 1922	Windernere	0.048	—	0.007	2.4	0.84	4.3 (K+Na)	0.2	59.8
Clarke, 1924	Amazon	0.2	0.04	0.00	4	0.52	1.36	1.15	—
Clarke, 1924	Nile	—	tr.	1.25	12.45	1.63	1.76	1.57	37
Dole, 1909	Mississippi	0.098	0.023	1.52	15.6	5.25	1.7	5.1	11.9
Collins, 1910	Mississippi	0.32	—	0.07	33.8	9.4	13.4	34	17.4
Wiebe, 1931	Mississippi	0.61	—	0.61	44	8.4	10 (K+Na)	11	16.6
W. R. B. 1930	Wharf	0.91	0.05	tr.	—	16 (K+Na)	21 (K+Na)	24	26.9
Koffoid, 1903	Illinois	1.58	0.022	—	32	2.1	—	—	—
Collins, 1910	Illinois	2.82	0.023	0.15	72	13.2	3.4	11.3	34.4
Thresh <i>et al.</i> 1933	Illinois	9.5	—	0.32	55.1	27.2	6.5	42.2	26.1
Thresh <i>et al.</i> 1933	Thames at Slough	11.3	—	0.21	107	28.7	20	18 (K+Na)	31.6
Pearsall, 1922	Welland	3.5	—	0.27	50	21	18 (K+Na)	12	39.8
Atkins 1923, 1924 (h)	Trent	1.98	—	—	86.5	4.8	—	—	26.7
Tressler & Domogalla, 1931	Various	1.65	—	—	184	45.5	85 (K+Na)	15.5	—
Juday <i>et al.</i> 1927, 1931	Lake Wingra	tr.	0.02	—	—	—	—	—	32.7
Harris & Silver, 1940	Wisconsin Lakes	0.25	tr.	0.015	0.54	—	—	—	—
Pearsall, 1922, 1930	Texas Reservoir Lakes	0.44	0.04	0.005	—	—	—	—	—
Pearsall, 1922, 1930	English lakes	0.016	0.005	0.01	0.2	0.7	—	—	0.1
Selected typical fresh waters	tr.	0.2	0.04	0.32	6.3	3.1	tr.	—	30.6
M. W. B. 1937	30 surface waters (f)	2.0	—	—	1.59	0.81	5.6	tr.	75.9
M. W. B. 1937	36 well waters	0.8	0.02	—	184	45.5	—	—	19.3
Clarke, 1924	Various collection	5.0	0.137	—	—	—	—	—	19.2
Thresh <i>et al.</i> 1933	Surface waters (e)	0.1	0.003	—	—	—	—	—	7.34
Murray, 1887	Average of surface waters (g)	8.7	0.064	2.06	490	1.3	0.03	0.03	0.6
Clarke, 1924	Average of surface waters (g)	0.31	0.2(c)	3(d)	31	273	—	379	40
—	—	—	—	—	—	—	31	33.5	66.6
—	—	—	—	—	—	tr.	—	750	—
—	—	—	—	—	—	—	—	13	13.3
—	—	—	—	—	—	—	—	5	9.3
—	—	—	—	—	—	—	—	3	2.4
—	—	—	—	—	—	—	—	8.8	0.3
—	—	—	—	—	—	—	—	—	16.4
—	—	—	—	—	—	—	—	—	152 (c)
—	—	—	—	—	—	—	—	—	152

The figures give the range, the upper being the maximum and the lower the minimum; when only one figure is given, it represents an average; tr. = trace; (a) River Thames at Staines; (b) maximum P at 20 m. depth; (c) figure from Pearsall (1922); (d) including aluminium; (e) exclude Thanes at Grays; (f) average for the year; (g) calculated with 152 as the average salinity; W. R. R. B., West Riding River Board; M. W. B., Metropolitan Water Board, London; (h) Atkins & Harris (1924).

There seems evidence of a slight deficiency of P in a concentration of 0.5 p.p.m., even during the short period of 2 weeks. It is clear that the concentrations of both  $\text{NH}_4\text{NO}_3$  and  $\text{K}_2\text{HPO}_4$  in 1/4 and 1/8 Benecke (Exp. 3) are more favourable than higher concentrations. The  $\text{K}_2\text{HPO}_4$  concentration in 1/16 and 1/32 Benecke's solution (about 3 and 1.5 p.p.m. respectively) is not less favourable than higher concentrations. The poor growth in these concentrations of Benecke's solution must be therefore due to deficiency of one or more of the other salts.

A combination of  $\text{K}_2\text{HPO}_4$  1 p.p.m. and  $\text{NH}_4\text{NO}_3$  25 p.p.m. is thus specially suitable for *Pediastrum*. Parallel cultures were made in a solution (medium 1, see p. 298) with these concentrations of phosphate and nitrate, together with 25 p.p.m. of  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  and of  $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$  and 0.5 p.p.m. of  $\text{FeCl}_3$ , as well as with undiluted and with 1/2, 1/4 and 1/8 Benecke. The best growth was obtained with medium 1. The concentrations of the various elements in medium 1 are similar to those of certain natural waters (see Table 7).

(d) *The influence of the source of nitrogen*

Medium 1 contains ammonium and nitrate N. In order to ascertain which is the more suitable source of N, three further solutions (media 2, 3 and 4, p. 298) were prepared by replacing  $\text{NH}_4\text{NO}_3$  by equal amounts of  $\text{KNO}_3$ ,  $(\text{NH}_4)_2\text{SO}_4$  and  $(\text{NH}_4)_2\text{HPO}_4$  respectively.

Exp. 5. Three drops with approximately 2300 colonies from a culture in medium 1 inoculated in duplicate series into 10 c.c. of each of the media 1-4; 7 hr. daily illumination (apparatus C).

The duplicate series showed close correspondence. The results of one of them after 18 days are given in Table 8.

Table 8

Medium	Source of N	Total area of colonies per c.c. (unit = $86,600\mu^2$ )
1	$\text{NH}_4\text{NO}_3$	179
2	$\text{KNO}_3$	158
3	$(\text{NH}_4)_2\text{SO}_4$	148
4	$(\text{NH}_4)_2\text{HPO}_4$	155

Although the amount of nitrogenous salt in each medium is the same, the actual N content differs. Thus, in medium 2 the N concentration is less than half that in medium 1, so that with equal amounts of N,  $\text{KNO}_3$  seems to support better growth, although the difference is not large enough to admit of a definite conclusion. The experiment, however, shows that good growth can be obtained whether the N is supplied as nitrate or as ammonium salt.

At the same time two cultures were made under similar conditions with medium 3 without phosphate. There was scarcely any growth. After 3 weeks the cultures were tested for ammonia and nitrate. A marked orange precipitate was obtained with Nessler's reagent, but no blue colour was observed with diphenylamine (1% in 77%  $\text{H}_2\text{SO}_4$ ). This indicates that nitrification was not taking place in the medium. Hence *Pediastrum* must derive its N directly from the ammonium in media 3 and 4 in Exp. 5.

(e) *The preparation of media for the culture of Pediastrum*

*Pediastrum Boryanum* is present at most times of the year in many natural waters. The quantity and relative proportions of the salts in them must be suitable for its growth at the time of its maximum abundance and reasonably suitable at other times. Five coenobia

were inoculated into 10 c.c. of sterilized water from the Barn Elms Reservoir, Hammer-smith, where *Pediastrum* is never abundant, as well as into 10 c.c. of the same water with the addition of 25 p.p.m. of  $(\text{NH}_4)_2\text{SO}_4$ ; exposure to 7 hr. artificial illumination (apparatus A) per day afforded good growth in the latter, while in the former growth was poor, although some multiplication did take place. There seems to be insufficient N in this water for an abundant development of *Pediastrum*.

Certain salts, which are commonly present in natural waters, are lacking in the artificial solutions so far used. The most important are carbonates and silicates, which often occur in considerable quantities and may well play some role in the growth of planktonic algae. My aim was to prepare a solution resembling that found in natural waters as closely as possible, since only then could the results of experimentation be applicable to problems confronting water undertakings and fisheries. Taking into consideration the analyses of a number of natural waters and the results of the previous experiments, a further medium (5) was prepared which has a composition very similar to that of ordinary fresh waters. *Pediastrum* grows better in this solution than in any of those previously tested.

The single source of N in it ( $(\text{NH}_4)_2\text{SO}_4$ ) is present in the same amount as in medium 3. The phosphate concentration (5 p.p.m.) is five times as great as in media 1-4, in order to ensure that there shall be no P deficiency in cultures of longer duration, such a concentration having been shown to be suitable for *Pediastrum* in Exp. 4. For stock solutions, 100 p.p.m. of  $(\text{NH}_4)_2\text{SO}_4$ , without changing the amount of other constituents, has proved very satisfactory, this solution being very suitable also for growing class material. The concentration of  $\text{Cl}_2$  and  $\text{SiO}_2$  is about the same as the average in the surface waters analysed by the Metropolitan Water Board Laboratory during 1937. The amount of NaCl and anhydrous  $\text{MgSO}_4$  is approximately equal to that in the Illinois (Kofoid, 1908, p. 234). The amount of  $\text{CaCO}_3$  is that commonly found in the English silted lakes (Pearsall, 1930).

Medium 5 was used extensively in experiments with *Pediastrum* and certain other planktonic algae, although it was subsequently found that concentrations of  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 25 p.p.m., and NaCl, 1 p.p.m., afforded better growth. A modification of medium 5 (medium 6) was specially prepared for experiments on the effect of different concentrations of N on the growth of *Pediastrum*. Variation in the amount of  $(\text{NH}_4)_2\text{SO}_4$  in medium 5 entails not only a change in N concentration, but also in  $\text{SO}_3$  concentration. In medium 6 the nitrogenous salt is therefore  $\text{NH}_4\text{Cl}$ , and NaCl is replaced by  $\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$ , the amount of the latter being such that the amount of  $\text{SO}_3$  is the same as in medium 5, although there is less Na than in the latter. *Pediastrum* thrives also in this medium, the suitable range of concentration of  $\text{NH}_4\text{Cl}$  being 0·01-0·05 g./l.

In medium 7 nitrate replaces ammonium as a source of N, while  $\text{Na}_2\text{CO}_3$  replaces  $\text{CaCO}_3$ , sufficient Ca being provided by the  $\text{Ca}(\text{NO}_3)_2$  present. The N content is the same as in medium 5. *Pediastrum* grows equally well in this solution, a point which furnishes further confirmation of the fact that it can use both nitrate and ammonium as a source of N.

NaCl is regularly present in natural waters, and even rain water always contains a certain amount of it (Thresh, Beale & Suckling, 1933, p. 7). Experiments with concentrations from zero upwards, however, indicate that NaCl is not essential for the growth of *Pediastrum*. In concentrations above 10 p.p.m., which are common in natural waters, it exerts a detrimental effect. Silicates are also not indispensable for the growth of *Pediastrum* and with concentrations of about 50 p.p.m. (or  $\text{SiO}_2$  19·6 p.p.m.) upwards, which are not rare in natural waters, an increasing inhibiting or toxic effect is observable.

As a result of these findings another medium (8) was prepared in which there is no chloride or potassium silicate,  $\text{KNO}_3$  being used as the source of N to make up the amount of K, while  $\text{NaCl}$  and  $\text{Na}_2\text{CO}_3$  are replaced by  $\text{CaCl}_2$  and  $\text{K}_2\text{CO}_3$  respectively. There is no sodium salt in this solution, while the unnecessary amounts of phosphate and sulphate are diminished. The medium is less concentrated than the others, the total solid being less than 0·06 g./l. It has been used mainly for stock-cultures of *Pediastrum*, sometimes with the quantity of  $\text{KNO}_3$  doubled, and has proved very satisfactory.

*(f) Concentrations of the more important salts suitable for  
the growth of *Pediastrum Boryanum**

The effects of different concentrations of salts were examined in Exp. 6. Various media were used, including 9 and 10, which were prepared for the culture of *Nitzschia* and *Botryococcus* respectively, but which were found to be also suitable for *Pediastrum*.

Exp. 6. Seventeen duplicate series of cultures with different amounts of: (1)  $\text{KNO}_3$  in medium 8; (2)  $\text{NH}_4\text{NO}_3$  in 1/4 Benecke; (3)  $\text{NH}_4\text{Cl}$  in medium 6; (4)  $(\text{NH}_4)_2\text{SO}_4$  in 5; (5)  $\text{K}_2\text{HPO}_4$  in 6; (6 and 7)  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  in 7 and 9; (8 to 10)  $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$  in 2, 5 and 9; (11) and (12)  $\text{KCl}$  in 5 and 9; (13)  $\text{NaCl}$  in 5; (14 and 15)  $\text{K}_2\text{SiO}_3$  in 6 and 8; (16)  $\text{K}_2\text{CO}_3$  in 8; and (17)  $\text{FeCl}_3$  in 10. In each series the concentration of only one of the constituent salts was varied in the different cultures, the other conditions being the same. In examining the effects of different concentrations of calcium in medium 5,  $\text{CaCO}_3$  was replaced by  $\text{Na}_2\text{CO}_3$  (30 p.p.m.). Similarly,  $\text{Ca}(\text{NO}_3)_2$  and  $\text{CaCO}_3$  in medium 9 were replaced by  $\text{KNO}_3$  (20 p.p.m.) and  $\text{Na}_2\text{CO}_3$  (10 p.p.m.) respectively.

It is unnecessary to describe each series in detail, and a brief summary will suffice to give a picture of the concentrations of different salts and elements which allow of optimum growth. The lower and upper limits of concentration of N and phosphate for the multiplication of *Pediastrum* and other planktonic organisms are dealt with in the second part of this paper, where the full data are given. The effect of Ca, Mg, K, Na,  $\text{SiO}_2$  and Fe, together with their ratios and interreactions, will be discussed in later papers. Such results as have a bearing on the preparation of a more suitable medium for *Pediastrum* are summarized in Table 9.

The ranges of suitable concentrations given in this table do not imply that *Pediastrum* will fail to grow if these constituents are not present within the limits indicated. Better growth is, however, obtained if these limits are not exceeded. The lower limits given are generally a little higher than those actually affording an optimum growth. Concentrations at or just above the lower optimum limit, although permitting of good growth for a short period, are not suitable for cultures of longer duration, since the concentration soon falls below the lower limit.

Certain important indications concerning the nutritional requirements of *Pediastrum Boryanum* are given by this experiment. These may also be applicable to allied species, such as *P. pertusum*, as well as to other planktonic algae which are often associated with *P. Boryanum*. They are:

(1) The lower limit of N and P is well within that found in natural waters (cf. Table 7), although the upper limit is far beyond the natural range. These two elements are therefore always liable to be limiting factors for the development of *Pediastrum* in natural waters, when other conditions are suitable. The inhibiting effect of too high a concentration of N or P is unlikely to operate in nature.

(2) *P. Boryanum* favours concentrations of Ca, Na, and Mg which are lower than those found in most waters. The Mg, and especially the Ca content, of many natural waters is above the upper limit suitable for its growth. It can, however, resist high concentrations of K. Soft waters, therefore, seem to be more suitable for it than hard waters, if the Na concentration is not too high. There seems to be some inhibiting effect, when Na exceeds 4 p.p.m., but the effect is not serious, even with a concentration up to 200 p.p.m.

(3) The presence of silicates seems to be of no advantage. There is no inhibiting effect until the concentration of SiO<sub>2</sub> exceeds 4 p.p.m., but the harmful effect becomes very marked when SiO<sub>2</sub> reaches 39 p.p.m. or more.

Table 9. Summary, in p.p.m., of suitable concentrations of different salts and elements for the growth of *Pediastrum Boryanum*

Salts and elements	Suitable concentrations							Usual suitable range
	KNO <sub>3</sub>	NH <sub>4</sub> NO <sub>3</sub>	NH <sub>4</sub> Cl	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub>	K <sub>2</sub> HPO <sub>4</sub>	MgSO <sub>4</sub> .7H <sub>2</sub> O	CaCl <sub>2</sub> .6H <sub>2</sub> O	
KNO <sub>3</sub>	—	—	—	—	10-100	—	—	10-100
NH <sub>4</sub> NO <sub>3</sub>	—	—	—	—	—	—	—	10-50
NH <sub>4</sub> Cl	—	—	10-50	—	—	—	—	10-50
(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub>	—	10-25	—	—	—	—	—	10-25
K <sub>2</sub> HPO <sub>4</sub>	—	—	0-5-10	—	—	—	—	0-5-10
MgSO <sub>4</sub> .7H <sub>2</sub> O	—	—	—	25-50	—	1-10	—	25
CaCl <sub>2</sub> .6H <sub>2</sub> O	0-1-40	0-1-10	—	—	—	1-40	—	1-10
KCl	—	0-1-500	—	—	—	0-1-20	—	0-1-20
NaCl	—	0-1-5	—	—	—	—	—	0-1-5
K <sub>2</sub> SiO <sub>3</sub>	—	—	5-25	—	0-10	—	—	5-10
K <sub>2</sub> CO <sub>3</sub>	—	—	—	—	1-100	—	—	1-100
N	—	2-1-5	2-13	—	1-4-14	—	—	2-1-5
P	—	—	0-09-1-8	—	—	—	—	0-09-1-8
Ca	0-02-7-5	0-02-2	—	—	—	0-2-7-5	—	0-2-2
Mg	—	—	—	2-4-4-8	—	0-1-1	—	2-4
K*	—	12-4-274-3	—	—	—	13-6-24	—	13-6-24
Na	—	0-04-2	—	—	—	—	—	0-04-2
SiO <sub>2</sub>	—	—	2-9-8	—	0-3-9	—	—	2-3-9
Fe	—	—	—	—	—	0-02-0-8	—	0-02-0-8
Media	2	5	6	7	8	9	10	½ Benecke

\* The amount of K in Tables 9, 13 (p. 311), 18 (p. 316), 19 (p. 319), 20 (p. 321), 21 (p. 322) and 22 (p. 323) is the quantity contained in KCl and that contained in K<sub>2</sub>HPO<sub>4</sub> and K<sub>2</sub>SiO<sub>3</sub> in the original media used.

(4) Growth increases with increasing carbonate content up to 22 p.p.m. which seems to be the optimum concentration in the solution used. A concentration higher than 43 p.p.m. is definitely harmful. K<sub>2</sub>CO<sub>3</sub> is preferable to CaCO<sub>3</sub> as a source of carbonate.

(5) The suitable concentrations of an element may differ to a certain extent in different media. Thus, the range for N is larger when nitrate is used than when ammonium salts are used, and the suitable concentrations of Ca seem to be higher when there is less Mg.

As a result of Exp. 6, medium 11 was prepared in which the quantity of each constituent salt is adjusted so that it is well within the suitable range of concentration given in Table 9; at the same time the amounts are within or very near to the range found in natural waters. Medium 11 is much like 8, but contains silicate and is thus more like a natural water. It has been frequently used in my experiments.

## 2. *Staurastrum paradoxum* Meyen

The material, collected in January 1939 from the no. 8 Barn Elms Reservoir at Hammersmith, contained also *Closterium aciculare*, *Asterionella gracilima*, *Fragilaria crotonensis*, *Stephanodiscus astraea*, *Nitzschia acicularis*, *Melosira*, *Microcystis*, *Anabaena flos-aquae*, *Cryptomonas ovata*, and *Trachelomonas volvocina*.

*Exp. 7.* Preliminary tests were carried out as for *Pediastrum* (Exp. 1) with Benecke's, Bristol's, Czurda's, Pringsheim's (1912, 1914, 1926), Conrad's and Kufferath's solutions, each with and without 5 % of soil extract. Ten drops of the sample were introduced into 50 c.c. of each of the twelve solutions and all were exposed in apparatus A. The only generally suitable medium proved to be Benecke's solution with soil extract. In this *Staurastrum* and *Nitzschia* were present in some numbers, while *Anabaena*, *Microcystis*, *Asterionella*, *Fragilaria*, *Melosira* and *Closterium*, though scanty, were also found in good condition. In Benecke, without soil extract, *Staurastrum* showed only a poor growth. *Nitzschia acicularia* also grew well in a number of the other solutions.

Single individuals of *Staurastrum paradoxum*, inoculated into 10 c.c. of Benecke's solution with 5 % of soil extract in small Petri dishes, were placed in illuminating apparatus A. During the first 5 days there was no division, and at the end of a fortnight only 14–16 individuals were found in each culture. Fresh inoculations of single individuals were then made into 10 c.c. of the same medium contained in test-tubes which were suspended much nearer to the source of light. These cultures showed considerable multiplication and became green in 3 weeks. At first the *Staurastrum* cells accumulated at the bottom, but later much of the growth occupied the sides of the tubes away from the source of illumination, where the light would be concentrated as a result of refraction. The even distribution caused by slight shaking persists for several days. Ultimately, when the medium had become depleted of one or more of its constituents, the growth again sank to the bottom, but addition of a single drop (approximately 0·05 c.c.) of a 1 % solution of  $\text{NH}_4\text{NO}_3$  caused resumed multiplication, and the individuals became distributed along one side of the tube as before.

Further cultures were made from one of the preceding in 250 c.c. conical flasks, containing 100 c.c. of Benecke's solution with 5 % of soil extract, each being inoculated with ten individuals. Two cultures were placed under apparatus A ( $22 \pm 2^\circ \text{ C.}$ ), two others in apparatus B ( $9 \pm 1^\circ \text{ C.}$ ), exposed to light of about the same intensity as that in A, while a fifth was kept in a cold greenhouse exposed to natural illumination. All but the last became densely populated in a month's time, despite the marked differences in temperature. Thus, as in the case of *Pediastrum*, temperature does not seem to be an important factor in the growth of *Staurastrum paradoxum*, even when as great a range as  $8\text{--}24^\circ \text{ C.}$  is involved, although temperatures outside this range have not been tested. The effect of light is certainly much greater. *S. paradoxum* has been found in the Barn Elms Reservoir and elsewhere at temperatures varying between 2 and  $22^\circ \text{ C.}$

*Staurastrum* grows much more slowly than *Pediastrum*, probably owing to the different method of reproduction; subcultures of the former were consequently made only once a month.

#### (a) *The concentration of the culture solution*

Preliminary experiments were made to discover the effect of different concentrations of the medium on the growth of *Staurastrum paradoxum* and also to ascertain whether this alga will grow in an artificial medium of approximately the same concentration as a natural water.

*Exp. 8.* Duplicate cultures in various dilutions of Benecke (see Table 10), one series (A) with 1 % soil extract, another (B) without it; all in Petri dishes with 20 c.c. of medium and exposed in apparatus A. Duplicate cultures were also made in filtered and sterilized reservoir water with and without 1 % of soil extract. Inoculum in each culture, ten

individuals. After 2 weeks the solution in each culture, except nos. 1 and 9 (see Table 10), was replenished by adding 20 c.c. of double the strength of the medium in question; in cultures 1 and 9 an equal volume of the same solution was added.

This experiment (see Table 10) admits of the following conclusions:

(1) *Staurastrum paradoxum* will multiply in dilutions of Benecke with soil extract down to 1/32 or, without soil extract, down to 1/16, as well as or even better than in the normal strength: greater dilutions do not support good growth.

(2) A concentration of 1/16 Benecke, with or without soil extract, gives the best result. The most suitable medium is, therefore, even more dilute than that established for *Pediastrum*.

(3) The concentration of all the constituents in the most suitable dilution (1/16) of Benecke are within the range in which they are found in natural waters (see Table 7).

(4) The sterilized reservoir water, with soil extract, affords a better growth than in any of the dilutions of Benecke, though the same water without soil extract does not support any growth.

Table 10. Total number of individuals of *Staurastrum paradoxum* (average of duplicate cultures) in different dilutions of A, with and B, without Benecke soil extract

No. of culture	Degree of dilution	A				B				
		8 days	13 days	21 days	30 days	Degree of dilution	8 days	13 days	21 days	30 days
1	Benecke + 1% soil extract	24	30	160	1,500	Benecke without soil extract	42	52	280	340
2	1/2	27	33	560	1,650	1/2	42	135	1,100	1,100
3	1/4	29	50	1,000	3,000	1/4	28	120	920	1,120
4	1/8	93	234	1,400	5,000	1/8	53	175	1,300	1,300
5	1/16	127	231	1,500	11,600	1/16	90	400	1,500	2,100
6	1/32	50	72	450	3,630	1/32	37	50	100	110
7	1/64	22	24	30	30	1/64	31	40	60	80
8	1/128	20	20	30	30	1/128	20	20	20	20
9	Reservoir water + 1% soil extract	148	565	75,000	500,000	Reservoir water without soil extract	20	20	20	20

(5) The failure of cultures 1-8 of series A to afford as luxuriant a growth as 9 indicates that Benecke's solution and its various dilutions do not provide so good a base for the growth of this alga as the natural water with the addition of soil extract.

As a result of the experience gained in Exp. 8, an endeavour was made to grow *Staurastrum* in a solution similar to that afforded by natural waters. Medium 5 (p. 298) was found to be suitable for *Staurastrum*, which grew better in it than in Benecke, though not as well as *Pediastrum*.

#### (b) The source of nitrogen

Pringsheim classes organisms into three groups, (1) those that use nitrate N, (2) those that use ammoniacal N, and (3) those that can use both; he places *Staurastrum* in the second of these groups. Medium 5 contains ammonium as the source of N. It was therefore of interest to ascertain whether *S. paradoxum* could multiply when the ammonium salt was replaced by a nitrate.

Exp. 9. Three drops, containing about 500 individuals, from a culture in medium 5 were inoculated into duplicate 10 c.c. cultures in the same medium and into duplicate cultures in which the  $(\text{NH}_4)_2\text{SO}_4$  was replaced by an equal amount of  $\text{Ca}(\text{NO}_3)_2$ ; cultures

suspended around apparatus C. The average results from the duplicate cultures after 5 weeks are given in Table 11.

Table 11. *Staurastrum paradoxum*

Source of N	No. of cells per c.c.
$(\text{NH}_4)_2\text{SO}_4$	3712
$\text{Ca}(\text{NO}_3)_2$	3600

The growth in the two sets of cultures is approximately the same, from which it appears that *S. paradoxum* can use nitrate N as readily as ammoniacal N. Media 1-4, used in the culture of *Pediastrum*, were also tested and the desmid was found to grow in all of them. 20 c.c. of each medium were inoculated with twenty individuals. The growth after 12 days is shown in Table 12.

Table 12

Medium	Source of N	No. of individuals per c.c.
1	$\text{NH}_4\text{NO}_3$	360
2	$\text{KNO}_3$	280
3	$(\text{NH}_4)_2\text{SO}_4$	220
4	$(\text{NH}_4)_2\text{HPO}_4$	485

This also demonstrates that this desmid can utilize nitrate N. The results are therefore not in agreement with those of Pringsheim, and the failure of *Staurastrum* to grow on his agar medium with nitrate N must have been due to some other factor.

(c) *Concentrations of the more important salts suitable for the growth of Staurastrum paradoxum*

Exp. 10. *Staurastrum paradoxum* grows well in media 6-9 (p. 298), though the growth in 9 is better than in the others. The most suitable concentrations of important salts for the growth of this alga were investigated in the same way as for *Pediastrum* (see Exp. 6). Table 13 summarizes the results.

Table 13. *Summary, in p.p.m., of suitable concentrations of different salts and elements for the growth of Staurastrum paradoxum*

Salts and elements	Suitable concentrations					Usual suitable range
	—	—	—	—	—	
$\text{Ca}(\text{NO}_3)_2$	—	—	—	—	—	5-100
$\text{NH}_4\text{Cl}$	—	—	5-50	—	—	5-50
$(\text{NH}_4)_2\text{SO}_4$	—	10-50	—	—	—	10-50
$\text{K}_2\text{HPO}_4$	—	—	0.5-10	—	—	0.5-10
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	—	—	—	25-75	—	40-100
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	1-500 or more	10-100	—	—	—	1-500 or more
KCl	—	1-100	—	—	—	1-40
NaCl	—	0-60	—	—	—	0-60
$\text{K}_2\text{SiO}_4$	—	—	0-50	—	—	0-50
$\text{K}_2\text{CO}_3$	—	—	—	—	1-100	—
N	—	2-10	1.6-16	—	—	0.8-17
P	—	—	0.1-1.8	—	—	0.1-1.8
Ca	0.2-94 or more	0.2-19	—	—	—	0.2-94 or more
Mg	—	—	—	2.5-7	—	4-10
K*	—	12.8-64.7	—	—	—	14.1-34.5
Na	—	0-24	—	—	—	0-24
$\text{SiO}_2$	—	—	0-20	—	—	0-20
Media	2	5	6	7	8	9

\* See footnote under Table 9 (p. 308).

This experiment affords some important indications concerning the nutritional requirements of *S. paradoxum*:

(1) N in the form of  $\text{NH}_3$  has an inhibiting effect on its growth when the concentration is higher than 17 p.p.m., although in medium 9, with a concentration of nitrate N of 85 p.p.m., there is still moderate growth. It is unlikely that such an inhibiting effect ever comes into play in natural waters, where the concentration of inorganic N is generally much below these limits. The N content generally falls during the summer. Pearsall (1932) has shown that green algae develop during this period of lower nitrate and phosphate concentration, and that desmids tend to replace colonial green algae in late summer when the N and P are reduced to the lowest level. Under the conditions used in these experiments nothing indicates that *Staurastrum paradoxum* favours low concentrations of N and P, nor is there any evidence (cf. Exp. 6) that the colonial *Pediastrum* is adversely affected by concentrations of N and P higher than those found in the English lakes during early summer. Both organisms are favoured by a N concentration (Exps. 6 and 10) not lower than 0.7 p.p.m. and a P concentration not lower than 0.09 p.p.m., i.e. concentrations of N and P that are not reached in the English lakes.

(2) The concentrations of N and P in the culture media hitherto used are always in excess of the suitable range and must exercise an inhibiting effect. This is no doubt one of the reasons why such media failed to support good growth of this alga in Exp. 7. Since the P content of natural waters is as a rule below 1 p.p.m., it can be safely said that the growth of this desmid is never inhibited in nature by the presence of excessive phosphate. On the other hand, P and N deficiency must often be important factors limiting the growth of *Staurastrum paradoxum*, since the P content of the water often falls to a very low level during the summer and is sometimes so low that no phosphate is detectable. Under the temperature and illumination conditions in my experiments, there is very little multiplication in cultures with 0.018 p.p.m. of P and still less when the P content is lower.

(3) Contrary to what was established for *Pediastrum*, the Ca content of most fresh waters is generally within the optimum range for the growth of *Staurastrum paradoxum*. Desmids are known to favour low Ca concentrations, but for *S. paradoxum* a range as great as from 0.2 to 94 p.p.m. is suitable, although it may be smaller (0.2–19 p.p.m.) in media with a high Mg content such as medium 5. The occurrence of this desmid in natural waters both poor and rich in Ca (Pearsall, 1932) is evidently correlated with this fact. It occurs in Wastwater with a very low Ca content, as well as in Windermere with the highest Ca content of the eleven lakes studied by Pearsall. The range of Ca content in the Lake District is approximately from 1.7 to 7.2 p.p.m.

(4) The best growth occurs in cultures with a Mg content varying between 2.5 and 10 p.p.m. according to the medium, but fairly good growth is still obtained in concentrations outside this range, from much below 2.5 up to 50 p.p.m.; in the latter there is a certain degree of inhibition. Although the  $\text{MgSO}_4$  content in natural waters may be as much as or more than 3 g./l. (Thresh *et al.* 1933, p. 348), the Mg content of ordinary waters (0.8–45.5 p.p.m.; cf. Pearsall, 1922) is within the range of the experiment.

(5) The K content of most, if not all, fresh waters is below the upper limit of the suitable range for the growth of *S. paradoxum*.

(6) Na appears to be unnecessary for the growth of *S. paradoxum*, but there is no marked unfavourable effect in cultures containing up to 24 p.p.m., although there is an increased inhibiting effect in higher concentrations; the growth is very poor when the

concentration reaches 200 p.p.m. which may be exceeded in nature. The Na content of the fresh waters enumerated by Clarke (1924) is from 0·37 to 350 p.p.m. and that of British waters may exceed 1000 p.p.m. (Thresh *et al.* 1933, p. 388).

(7) The growth of *S. paradoxum* is slightly increased by increasing the SiO<sub>2</sub> content up to about 20 p.p.m., while from 29 p.p.m. upwards there is an inhibiting effect. The SiO<sub>2</sub> content of fresh waters usually varies between 0·3 and 19 p.p.m. (Pearsall, 1922), but may exceed 30 p.p.m. (Thresh, *et al.* 1933). In nature the development of *S. paradoxum* will be favoured in waters with a higher SiO<sub>2</sub> content, unless it is unusually high.

(8) The range of suitable concentrations of N and P is greater when N is supplied as nitrate than when ammonium salts are used.

By selecting the optimum concentration of each of the important elements as deduced from Exp. 10, medium 12 (see p. 299) was prepared; this is very like medium 7 which had previously been found to be suitable for *S. paradoxum*. The only important difference is the greater amount of K in medium 12, in which this desmid shows better growth than in any of the others. In preparing stock cultures to last for a longer period higher concentrations of nitrate are advisable. *S. paradoxum* showed almost equally good growth in medium 11 prepared for *Pediastrum*. It is surprising that this medium should be equally suitable for two organisms with such different nutritional requirements, especially as regards Ca. Of all the algae so far studied *Pediastrum* is the most susceptible to the unfavourable effect of higher concentrations of Ca, its growth often being inhibited by a concentration higher than 0·2 p.p.m., and a concentration of 91 p.p.m. usually proving fatal. *Staurastrum paradoxum*, on the other hand, which is very tolerant of high Ca concentrations, grows best in concentrations not lower than 0·2 p.p.m., which seems to be about the lower optimum limit. Thus the Ca concentration in medium 11 is just at the point where the optimum ranges for *Pediastrum* and *Staurastrum* coincide.

For experimental work the concentrations of nitrate and phosphate are best adjusted so as to be within the ranges found in natural waters. If higher concentrations have to be used, the N and P should not exceed 17 and 18 p.p.m. respectively.

The pH values of media 11 and 12 are 8·6 and 7·6 respectively. *S. paradoxum* seems to be able to withstand a wide range of pH values, being found in Norwegian waters with a pH ranging between 5 and 7·8 (Strøm, 1926) and in the Lake District with a pH between 6·4 and 7·4 (Pearsall, 1930, 1932).

### 3. *Botryococcus Braunii* Kutz.

This alga, isolated from a small artificial pond, grew well on agar made up with Knop's or Benecke's solution, with or without soil extract, as well as in the latter solution itself. Czurda's solution was also found to support good growth.

#### (a) *The concentration of the culture solution*

*Exp. 11.* In this experiment (Table 14) the effect of different dilutions of Benecke was tested. There is no marked difference during the first three weeks, as in this solution the growth of the alga is very slow. At the end of 7 weeks the growth in the more dilute solutions is not so good, and this becomes more marked at the end of 3 months, when the colonies in normal and 1/2 Benecke remain green, while those in the other dilutions become yellowish green. The change of colour and the diminished growth in the more

dilute solutions must be due to depletion of one or more of the important elements, especially N. To one of the 10 c.c. cultures in 1/64 Benecke 0.03 c.c. of 1%  $\text{NH}_4\text{NO}_3$  was added after it had become yellowish, and within 3 weeks it again assumed a green colour.

Table 14. *Growth of Botryococcus in various dilutions of Benecke, as estimated by turbidity*

Concentration of solution	Density of growth expressed as turbidity (see p. 295)		Colour of culture after 3 months
	3 weeks	7 weeks	
1	0.8	1.4	Green
1/2	0.8	1.1	Green
1/4	0.9	1.0	Yellowish green
1/8	0.85	1.0	Yellowish green
1/16	0.8	0.9	Yellowish green
1/32	0.8	0.8	Yellowish green
1/64	0.8	0.8	Yellowish green

(b) *The supply of nitrogen and phosphorus*

Exp. 12. In this experiment various media (see Table 15) were tested. Inoculum: 5 drops from a culture in Benecke, each drop containing on the average seventy colonies. Cultures suspended around apparatus C.

Table 15. *Growth of Botryococcus in various media  
(estimated by turbidity; for unit, see p. 297)*

Medium	Source of N	Density of growth		Size of colonies*
		10 days	35 days	
1	$\text{NH}_4$ and $\text{NO}_3$	0.65	1.3	s
2	$\text{NO}_3$	0.7	2.5	l
3	$\text{NH}_4$	0.65	1.3	s
4	$\text{NH}_4$	0.65	1.3	m
9	$\text{NO}_3$	0.7	2.0	l
Benecke	$\text{NH}_4$ and $\text{NO}_3$	0.65	1.2	s
½ Benecke	$\text{NH}_4$ and $\text{NO}_3$	0.65	1.0	s
Czurda	$\text{NO}_3$	0.65	1.3	l

\* s = small, m = medium, l = large.

The best growth was obtained in media 2 and 9 in which the colonies were large and numerous. It thus appears that nitrate is a better source of N than ammonia, provided the other constituents are present in suitable amounts, but *Botryococcus*, like *Pediastrum* and *Staurastrum*, will grow with either ammonia or nitrate, although larger colonies tend to be formed in media with nitrate. The better growth with nitrate N is especially well shown by that in media 1–4, in which all the constituents except the N-containing salts are the same. There is better growth in medium 2 in spite of the fact that the N content is the least. It cannot, however, be due to the low N content, since the growth is not decreased by addition of more nitrate. This is shown by the data given in Table 16.

Medium 2, with 10 times as much as  $\text{K}_2\text{HPO}_4$  and twice as much  $\text{FeCl}_3$ , was used in this experiment so that cultures would last longer without developing a phosphate or iron deficiency. Since, when the N concentration is constant, there is no marked difference in growth in cultures with  $\text{K}_2\text{HPO}_4$  concentrations varying between 0.5 and 100 p.p.m. until P deficiency occurs (see Table 17), an increase of P from 5 to 10 p.p.m. cannot appreciably modify the effect of the varying N concentrations indicated in Table 16.

The modification (medium 13, see p. 299) of medium 2, in which higher concentrations of  $K_2HPO_4$  (10 p.p.m.),  $FeCl_3$  (1 p.p.m.) and  $KNO_3$  (50 p.p.m.) are present, proved to be very suitable for the culture of *Botryococcus*. The content of N is 7 p.p.m. and, though high, is still within the range found in natural waters. The P concentration (1.8 p.p.m.) is about twice as high as that in Lake Wingra in November (Tressler & Domogalla, 1931), and much higher than that in most natural waters. As shown below (Table 17) such concentrations exert no inhibiting effect.

The capacity of *Botryococcus* to flourish in Benecke's and Czurda's solutions, in which *Pediastrum* and *Staurastrum* fail to grow properly, shows that it can tolerate higher concentrations of nitrate and phosphate than the other two algae. Its better growth with nitrate N is also noteworthy.

Table 16. *Growth of Botryococcus in medium 2 with different amounts of nitrate*

Conc. of $KNO_3$ , p.p.m.	Growth (as turbidity, for unit see p. 297)		
	34 days	107 days	203 days
0.1	0.2	0.3	0.3
0.5	0.4	0.45	0.45
1.0	0.5	0.65	0.73
2.5	0.8	1.75	2.5
5.0	0.85	2.7	3.7
7.5	0.85	4.3	6.0
10.0	0.85	4.6	7.0
25.0	0.9	—	—
50.0	0.85	7.2	14.0
100.0	0.5	7.0	13.0
500.0	0.3	1.7	9.0

Table 17. *Growth of Botryococcus in medium 2 in different P-concentrations*

Conc. of $K_2HPO_4$ p.p.m.	Density of growth (turbidity)		
	20 days	45 days	75 days
0.1	0.1	0.25	0.55
0.5	0.35	0.5	4.5
1.0	0.35	0.5	6.0
5.0	0.35	0.5	6.0
10.0	0.4	0.9	6.8
50.0	0.3	0.5	5.8
100.0	0.3	0.4	5.7
500.0	0.2	0.35	3.8

(c) *Concentrations of the more important salts suitable for the growth of Botryococcus Braunii*

Exp. 13. This experiment was conducted at the same time as Exp. 6 (p. 307). In testing the effect of Ca concentration, media 5 and 9 were modified as in Exp. 6. In testing K and Mg,  $Ca(NO_3)_2$ , 0.02 g./l., replaces  $KNO_3$  and  $CaCl_2 \cdot 6H_2O$  in medium 13, while  $KCl$ , 0.02 g./l., is added when the effect of Mg concentration is tested.

The results of this experiment (see Table 18) may be summarized as follows:

(1) The effect of Ca is significant, and to some extent differs in different media. There is an inhibiting effect during the first 37 days in all the media used when the concentration reaches 91 p.p.m., although this effect decreases in media 5 and 13 as the cultures grow older and disappears altogether after 85 days; though slightly reduced, it persists in medium 9 even after 85 days. The difference in growth in calcium concentrations varying from 0 (or a very little trace contained as impurities in the chemicals used) to 18.3 p.p.m.

is not significant during the first month in medium 9. After that there is better growth in the higher concentrations (7·3–18·3 p.p.m.) and after 85 days, that in 18·3 p.p.m. is better than in the others. In medium 5, *Botryococcus* grows better in the lower Ca concentrations (0·02–1·83 p.p.m.) during the first 37 days, but later on the optimum growth occurs in higher and higher Ca concentrations, the best growth after 85 days being in concentrations of 9·1–18·3 p.p.m. Such an apparent gradual change of optimum growth to higher Ca concentrations is no doubt due to the gradual consumption of Ca.

The variation in the effect of different Ca concentrations in different media seems to stand in some relation to the Mg content, especially during the first month. Optimum growth occurs in lower Ca concentrations when the Mg content is high, as in medium 5 (Fig. 8). The best growth in this medium (Mg=7 p.p.m.) is in Ca concentrations of 0·91–1·83 p.p.m.; in medium 13 (Mg=2·5 p.p.m.) in a Ca concentration of 10·9 p.p.m. and in medium 9 (Mg=1 p.p.m.) in Ca concentration of 14·7–18·3 p.p.m. The growth in different Ca concentrations in medium 13 is generally much better than in media 5 and 9,

Table 18. Summary, in p.p.m., of suitable concentrations of different salts and elements for the growth of *Botryococcus*

Salts and elements	Suitable concentrations			Usual suitable range
	—	—	—	
KNO <sub>3</sub>	—	—	—	10–100
K <sub>2</sub> HPO <sub>4</sub>	—	—	—	0·5–100
MgSO <sub>4</sub> .7H <sub>2</sub> O	—	—	0·40	0·5–100
CaCl <sub>2</sub> .6H <sub>2</sub> O	0·1–50	—	0·1–100	0·1–50
KCl	0·1–500	—	0·1–40	0·1–50
NaCl	0·1–500	—	—	0·1–500
K <sub>2</sub> SiO <sub>3</sub>	—	0·1–50	—	—
Na <sub>4</sub> CO <sub>3</sub>	—	—	—	0·1–50
N	—	—	—	0·1–100
P	—	—	—	0·1–14
Ca	0·02–9·4	—	0·02–18·7	0·02–18·7
Mg	—	—	0·3–8	0·2–8
K*	12·4–274·3	—	13·6–34·5	4·6–30·7
Na	0·04–19·5	—	—	0·04–19·5
SiO <sub>2</sub>	—	0·04–19·6	—	—
Media	5	6	9	13

\* See footnote under Table 9 (p. 308).

and the poorest growth in the former is better than the best in 9 with Ca concentrations from a very little trace as impurities to 18·3 p.p.m. Generally speaking, *Botryococcus* grows better with higher concentrations of Ca than does *Staurastrum paradoxum* in any of the above solutions.

(2) *Botryococcus* grows best in lower concentrations of Mg, although there is no marked inhibiting effect, even when the Mg reaches 4·8 p.p.m. In medium 9 concentrations up to 7·2 p.p.m. definitely inhibit growth.

(3) The low concentration of K in medium 9 favours the growth of *Botryococcus*. The best growth occurs in K concentrations below 34·5 p.p.m., while higher concentrations are unfavourable and a concentration of 58 p.p.m. is very harmful. In medium 5, where there is more than three times (7·0 p.p.m.) as much Mg as in medium 9, however, the growth in K concentrations of 56–274 p.p.m. is even better than in lower concentrations. The high concentration of Mg in medium 5 is ordinarily unfavourable to *Botryococcus*, but it is possible that K neutralizes this unfavourable effect, the presence of it in excess resulting in a balanced condition.

(4)  $\text{SiO}_2$  is harmful in concentrations above 29 p.p.m. which are sometimes surpassed in natural waters (e.g. in the Illinois the range is 26·1–31·6 p.p.m.), where an unfavourable effect is to be expected.

(5) Na causes no injurious effects, even in the highest concentrations used in the experiment. The growth of *Botryococcus* in medium 5 is slightly increased by increasing the Na concentration. This again, as in the case of K, may be due to an antagonistic effect in the presence of a harmful concentration of Mg.

(6) The suitable range for all the substances mentioned, with the probable exception of Na and K in certain media, is narrower than that met with in natural waters and is

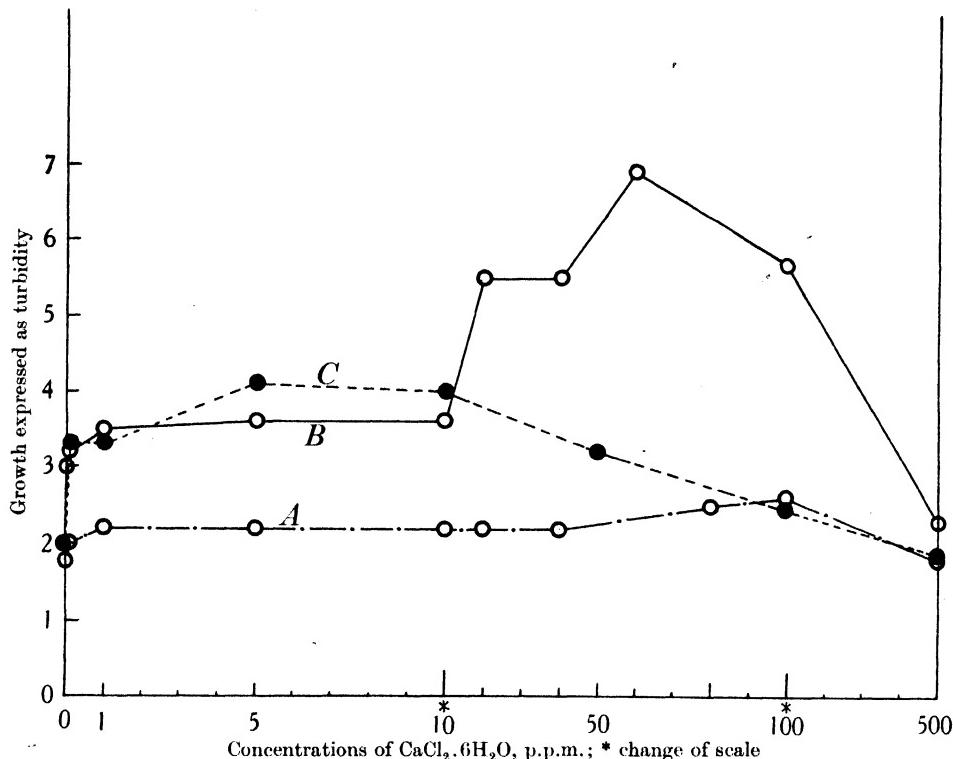


Fig. 8. Effect of different calcium concentrations in media with different magnesium concentrations on the growth of *Botryococcus Braunii*: A, medium 9 with 1 p.p.m. of magnesium; B, medium 13 with 2·5 p.p.m. of magnesium; C, medium 5 with 7 p.p.m. of magnesium (37 days, Exp. 13).

generally above the lower limits of the natural range. Under natural conditions, therefore, *Botryococcus* is unlikely to suffer from a deficiency of these elements, although their presence in higher concentrations in certain waters must have an unfavourable effect upon its growth, unless this effect is counterbalanced by the presence of suitable amounts of other antagonistic ions.

(7) The upper limit of the suitable range of concentrations of N and P, on the other hand, is much higher than those occurring in natural waters, so that *Botryococcus*, like *Pediastrum* and *Staurastrum*, will never suffer from too high a concentration of N and P in nature, although their deficiency will frequently limit its growth. In making stock cultures higher concentrations of N and P are advisable; 14 mg. of N and 9 mg. of P per litre can be used without any marked harmful effect.

Medium 10, which proved suitable for the growth of *Pediastrum* (p. 307), was first prepared for *Botryococcus*; it contains the optimum concentrations of each salt as deduced from experiment 13 and is very suitable for its culture; medium 13 is also satisfactory, and both can be used for stock cultures as well as for experiments. In them growth will continue for at least 3 months in 50 c.c. cultures, if the inoculum consists of about 500 colonies or less.

#### 4. *Nitzschia acicularis* and *N. palea*

##### (a) *Nitzschia acicularis*

As shown in Exps. 1 and 7, *N. acicularis* grows more readily in artificial media (viz. Benecke's, Czurda's, Knop's, and Richter's solutions with and without soil extract as well as on agar media made up with these solutions) than any of the other planktonic forms so far tested. It multiplies more rapidly than the other organisms present, and on agar often spreads to the outermost edge of the populated area. Single *Nitzschia* individuals often move some distance away from the main growth and thus offer good material for isolation. Pure cultures are also easily obtained by means of the washing method (p. 286). The first cultures were made in Benecke's solution with and without soil extract. Growth in 1/2 and 1/4 Benecke is better than in the full strength and in other dilutions, while in the presence of soil extract the best growth is obtained in dilutions of 1/8 and 1/16. A concentration of the medium, approaching that of natural waters, is therefore more suitable.

Medium 9, which has been used for growing *Pediastrum*, *Staurastrum* and *Botryococcus*, was first prepared for *Nitzschia acicularis*, being based mainly on the analysis of the Barn Elms Reservoir between November 1937 and May 1938, during which time this diatom was common. The amount of  $\text{Ca}(\text{NO}_3)_2$  at first used was 4 p.p.m., giving a N concentration (0.68 mg./l.) approximately equal to the average total ammoniacal and nitrate N in the reservoir. Later, *Nitzschia* was found to grow better in higher N concentrations and 40 p.p.m. of  $\text{Ca}(\text{NO}_3)_2$  was substituted. The amount of  $\text{SiO}_2$  roughly corresponds to the mean concentration in the reservoir, while the phosphate concentration is approximately that found during October when *N. acicularis* begins to show an increase. Its occurrence indicates that it grows better in higher P concentrations, since it began to decrease after the P content had fallen to its lowest level in April 1938. The Mg and Ca contents of the reservoir are not known. The amount of  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$  in medium 9 is the same as in 1/4 Benecke, while that of  $\text{CaCO}_3$  is the same as in medium 5. 1 p.p.m. of  $\text{FeCl}_3$  was found to be very suitable.

Medium 14 (see p. 299) is a modification of 9 approaching more nearly to natural waters. Bicarbonate is added, as well as an amount of chloride ( $\text{NaCl}$  40 p.p.m.) approximately equal to the average found in surface waters (M. W. B. 1937). *N. acicularis* grows well both in 9 and 14. In order to ascertain whether this diatom can use ammoniacal N,  $\text{Ca}(\text{NO}_3)_2$  in medium 14 was replaced by  $(\text{NH}_4)_2\text{SO}_4$ . The modified solution (medium 15) proved to be very satisfactory.

##### (b) *Nitzschia palea*

This diatom was isolated from the stream leading into the pond in the Cambridge Botanic Garden. It behaved like *N. acicularis* on agar and grew well in all the media suitable for that species.

*Exp. 14.* This is parallel with Exps. 6, 10 and 13, and has as its purpose the determination of the suitable concentration of each of the important salts for the growth of *N. palea*. Table 19 is a brief summary of the results.

As in the case of the organisms previously investigated, the suitable concentrations of N and P for *N. palea* exceed the range occurring in natural waters. A limiting effect due to deficiency must be frequent, but an inhibiting effect as a result of high concentrations will be rare, though it may occur near the bottom mud on which this diatom is often abundant. Certain striking features concerning other mineral requirements of this species are detailed below.

(1) It withstands higher concentrations of Mg than the algae previously dealt with, the optimum range including the highest concentration used in the experiment (48 p.p.m.). In cultures with not more than 0·1 p.p.m. of  $MgSO_4 \cdot 7H_2O$  the effect of Mg deficiency is very marked—a striking contrast to *Botryococcus*—but increase of the Mg concentration above the necessary minimum makes little difference. Although the Mg content may be

Table 19. *Summary, in p.p.m., of suitable concentrations of different salts and elements for the growth of Nitzschia palea*

Salts and elements	Suitable concentration				Usual suitable range
$Ca(NO_3)_2$	—	—	5-100	—	5-100
$NH_4Cl$	—	5-50	—	—	5-50
$(NH_4)_2SO_4$	24-50	—	—	—	24-50
$K_2HPO_4$	—	0·5-10	0·5-50	1-50	1-10
$MgSO_4 \cdot 7H_2O$	—	—	1-500	—	1-500
$CaCl_2 \cdot 6H_2O$	—	—	5-100	—	5-100
KCl	—	—	0-20	—	0-20
$K_2SiO_3$	—	25-100	—	—	25-100
N	5-10-5	1·6-16·5	0·8-17	—	5-10-5
P	—	0·09-1·8	0·09-9	0·2-9	0·2-1·8
Ca	—	—	0·9-18	—	0·9-18
Mg	—	—	0·1-48	—	0·1-48
K*	—	—	13·6-24	—	13·6-24
$SiO_2$	—	9·8-39	—	—	9·8-39
Media	5	6	9	14	—

\* See footnote under Table 9 (p. 308).

as low as 0·03 p.p.m. (Lake Superior), this diatom is unlikely to be affected by a deficiency or excess of Mg in most natural waters.

(2) The suitable range of Ca concentration is also wide; the optimum is apparently between 1 and 2 p.p.m., although good growth is still obtained in concentrations ranging from 3·7 to 18·7 p.p.m., if other conditions are suitable. On the other hand, *Nitzschia palea* seems to favour concentrations of Mg below 23 p.p.m.

(3) As is to be expected, there is a marked difference between the silica requirement of *Nitzschia* and that of the green organisms studied. While their growth is markedly inhibited when the silica content exceeds 19·6 p.p.m., the optimum concentration for the diatom is 29·4 p.p.m. When the concentration reaches 196 p.p.m., an inhibiting effect becomes apparent, but this probably never realized in natural waters. In cultures with silica below 0·4 p.p.m. the amount of growth decreases. Most fresh waters have a higher concentration than this, so that silica deficiency must operate far less frequently than in sea water. At certain times, however, when the silica concentration falls considerably below this level as a result of abundant diatom growth (as in Windermere and Bassenthwaite during summer), silica must become a limiting factor.

The mineral requirements of *Nitzschia palea* are more like those of *Staurastrum paradoxum* than those of *Pediastrum* or *Botryococcus*. Medium 16, which was prepared for *Nitzschia palea*, resembles medium 12 prepared for *Staurastrum paradoxum*, except in the higher Ca content of the former. Both support good growth of *Nitzschia*, but 16 is the more satisfactory. Parallel cultures of *N. palea*, made in media 9 ( $\text{Ca}(\text{NO}_3)_2$  40 p.p.m.), 12 and 16, at first showed the best growth in 9, but after 14 days that in 9 and 12 was approximately equal, being better than in 16, while at the end of 6 weeks there was better growth in 16 than in 12. The cells in both these cultures were normal with prominent yellow chromatophores, while those in 9 were very pale. The sequence shown by the growth in these media is of interest. All the constituents are present in suitable concentrations, the main difference lying in the amount of Mg and Ca; medium 12 has the highest Mg, while 16 has the highest Ca concentration. Either concentration may at first slightly delay growth, though this improves later. Media 12 and 16 are therefore specially suitable for cultures of longer duration, while 9 allows of a quick growth for a short time. *Nitzschia* grows well on agar media made up with any of the above solutions.

##### 5. *Fragilaria crotonensis*

This diatom, isolated from the Barn Elms Reservoir, is not as easy to grow as *Nitzschia*. Cultures in Benecke with 5 % soil extract and on agar made up both with this solution and with Knop's solution, afforded only very slow growth. It was soon established that *Fragilaria* grew better in media 5, 6, 9, 14 and 15 than in Benecke. The use of five different concentrations of  $\text{K}_2\text{HPO}_4$  (0.27, 1.0, 5, 10 and 50 p.p.m.) in medium 5 showed that the middle three are more suitable than the first and that *Fragilaria* grows better in higher concentrations of phosphate than are found in most natural waters; a concentration of 50 p.p.m. is, however, too high and results in poor growth. The ribbons in the solution with 10 p.p.m. were noticeably longer. Different concentrations of  $(\text{NH}_4)_2\text{SO}_4$  were then tested, and both in media 5 and 6 concentrations between 5 and 50 p.p.m. afforded better growth than concentrations below or above this range. *Fragilaria* grows equally well in media in which the N-containing salts are  $(\text{NH}_4)_2\text{SO}_4$ ,  $\text{NH}_4\text{Cl}$  or  $\text{Ca}(\text{NO}_3)_2$ .

*Exp. 15.* The suitable concentrations for the growth of *Fragilaria crotonensis* were determined in the same way as for *Nitzschia palea*. The results are summarized in Table 20.

The mineral requirements of *Fragilaria* resemble those of *Nitzschia*, although there are certain differences. The concentration of N supporting a moderate growth of *Fragilaria crotonensis* is slightly less, since it grows better than *Nitzschia palea* in a N concentration of 1 p.p.m. An inhibiting effect is very marked in both diatoms as soon as the N concentration reaches 33 p.p.m. *Fragilaria crotonensis* favours higher Ca concentrations than *Nitzschia*, the optimum reaching the highest concentration (91 p.p.m.) used in the experiment. On the other hand, the upper limit of suitable Mg concentrations is lower than for *Nitzschia*. The range of K and silica concentrations is approximately the same for both.

A comparison of the formula of medium 16 with Table 20 shows that the concentrations of salts in this medium are all within the ranges suitable for *Fragilaria crotonensis*, except that more growth might be expected if the quantity of silicate were increased. The most prolific growth of *Fragilaria* in medium 16 after 3 months is obtained when the amount of potassium silicate is 75 p.p.m., while with 50 and 25 p.p.m. the growth is proportionally

less. During the first month the growth in the lower silica concentrations is better, but after 2 months that in the higher concentrations becomes equal to it, so that a concentration of 75 p.p.m. of potassium silica seems to have a slight inhibiting effect until some of it has been absorbed.

Parallel cultures with media 9, 12 and 16 over a period of 3 months always resulted in the best growth of *Fragilaria* being obtained in the last. Three weeks later, however, the growth in medium 16 became white, probably as a result of depletion of N, while that in 9 and 12 still retained the normal yellow colour. The ribbons in 16 are longer than those in 9 and 12, especially during the first 2 weeks. The three media are therefore as satisfactory for *Fragilaria* as for *Nitzschia*, although cultures of the former in 9 and 12 last longer. The fact that retardation of growth does not occur in medium 16 as it does with *N. palea* must be due to the capacity of *Fragilaria cotonensis* to withstand a wider range of Ca concentrations. For general purposes this medium is that best suited for growing *F. cotonensis*.

Table 20. *Summary, in p.p.m., of suitable ranges of concentration of different salts and elements for the growth of Fragilaria cotonensis*

Salts and elements	Suitable concentration			Usual suitable range
	5-50	—	—	
$(\text{NH}_4)_2\text{SO}_4$	—	1-10	—	1-10
$\text{K}_2\text{HPO}_4$	—	5-50	—	5-50
$\text{NH}_4\text{Cl}$	—	—	1-100	1-100
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	—	—	0.1-500	0.1-500
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	—	—	0.1-100	0.1-100
KCl	—	—	—	—
$\text{K}_2\text{SiO}_3$	—	50-100	—	50-100
N	1-10.5	1.65-16.5	—	1.65-10.5
P	—	0.2-1.8	—	0.2-1.8
Ca	—	—	0.02-93.5	0.02-93.5
Mg	—	—	0.1-9.6	0.1-9.6
K $\ddagger$	—	—	13.6-66	13.6-66
$\text{SiO}_2$	—	19.6-39	—	19.6-39
Media	5	6	9	—

\* See footnote under Table 9 (p. 308).

It also grows well in medium 10 and on agar made up with it. 1 % of a micrometabolic elements solution (p. 299) added to medium 15 afforded an improvement in growth, the ribbons being longer (mostly with 30-60 cells) than in medium 15 without this solution. It is hoped later to investigate what elements in the solution are responsible for this effect. The micrometabolic elements solution was modified from that used by Trelease & Trelease (1935) by omitting  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ,  $\text{As}_2\text{O}_3$ ,  $\text{NaCl}$  and  $\text{NiCl} \cdot 6\text{H}_2\text{O}$  and using  $\text{AlCl}_3$  instead of  $\text{Al}_2(\text{SO}_4)_3 \cdot 18\text{H}_2\text{O}$ . The concentration was about 0.1 % of that in their stock solution.

## 6. *Asterionella gracillima*

Material, isolated from the Barn Elms Reservoir and from Lake Windermere, grew well in medium 9. With a primary inoculum of sixty-five colonies into 10 c.c. of this medium, a population of about 150,000 cells per c.c. is usually obtained in about 25 days; most of the colonies are eight-celled. Healthy growth is also obtained with one-tenth of the amount of calcium nitrate, but it is not so vigorous and, with a similar inoculum, only two-thirds as many colonies develop in the same period and most of them are four-celled.

Exp. 16. The tests to determine the suitable concentrations of the important constituents of the medium are summarized in Table 21.

Except for K and silica the range of suitable concentrations approximately coincides with those for *Fragilaria*. While there is no marked influence of a K concentration of 53 p.p.m. on *Fragilaria*, the harmful effect is very pronounced with *Asterionella*, the growth decreasing progressively when the K concentration exceeds 21 p.p.m. The optimum growth of *Fragilaria* takes place with a silica concentration of 29-39 p.p.m., while such concentrations are markedly harmful to *Asterionella*. The preference for higher concentrations of Ca is even more marked than in *Fragilaria*.

The ingredients in media 9-12 are all within the suitable range established by Exp. 16, and *Asterionella* grows well in all of them. An attempt was made to grow it in medium 11 with NH<sub>4</sub>Cl in place of KNO<sub>3</sub> (medium 17) in order to reduce the K concentration of the solution. Though the growth was good, many of the colonies showed a tendency to arrange their cells in longer or shorter ribbons after the fashion of *Fragilaria*; there were twenty-five or more cells in the ribbons which were frequently more or less curved and sometimes showed transitional stages between the normal and star-shaped arrangements.

Table 21. Summary, in p.p.m., of suitable concentrations of various salts and elements for the growth of *Asterionella gracillima*

Media	Ca(NO <sub>3</sub> ) <sub>2</sub>	K <sub>2</sub> HPO <sub>4</sub>	CaCl <sub>2</sub> .6H <sub>2</sub> O	MgSO <sub>4</sub> .7H <sub>2</sub> O	KCl	K <sub>2</sub> SiO <sub>3</sub>
9	10-100	1-50	1-500	0-1-80	0-1-10	—
6	—	—	—	—	—	25-50
Media	N	P	Ca	Mg	K*	SiO <sub>3</sub>
9	1-7-17	0-18-9	0-18-91	0-01-7-6	13-6-18-7	—
6	—	—	—	—	—	9-8-19-6

\* See footnote under Table 9 (p. 308).

In parallel cultures with media 9, 10, 11, 12 and 17, the best growth during the first week is in 9 and after 5 weeks in 10, that in 9 then being second best; subsequently the chromatophores in both cultures begin to lose colour and at the end of 10 weeks the cultures in 11 and 17 showed the best growth, while the cells in 9 and 10 were white or nearly so. At the end of 4 months the culture in medium 12 alone remained yellow. The rapid diminution in growth in media 9 and 10 is no doubt due to the small amount of K present. They are most suitable when a quick growth is needed, while medium 12 is to be recommended for cultures of longer duration. For general purposes medium 10 is advisable, since there is not much retardation of growth at first and the medium is able to support growth for a moderately long period. With an inoculum of about 100 cells in 10 c.c. of the medium the culture will remain in good condition for at least 6 weeks. If cultures are made with medium 9 every 3 weeks, with 11 every 8 or 9 weeks and with 12 every 3 months, the organism can be maintained indefinitely, provided the inoculum is not too large and the light-intensity suitable.

*Asterionella gracillima* grows well on agar (1-1.5%) made up with any of these five media. The cells are again arranged in straight or curved ribbons, and this feature is more marked here than in the liquid medium 17. The degree of curvature increases with decrease in the consistency of the agar, and in the more or less liquefied portion adjacent to the glass, star-shaped or half-star-shaped colonies, generally with a larger number of cells than in a liquid medium, are found. The growth is not as quick as that of *Nitzschia*, but is visible

to the naked eye within a month's time. Failure to cultivate *Asterionella* on solid media (M. W. B. 1937) is perhaps due to unsuitability of the medium used.

### 7. *Tabellaria flocculosa*

This species, isolated from Windermere, grows well in medium 9. As with other diatoms it withstands high concentrations of Ca, but grows better with lower concentrations of K. There is no inhibiting effect when the concentration of Ca is as high as 91 p.p.m. (cf. *Fragilaria*), but the difference between cultures with only a trace and those with as much as 500 p.p.m. of  $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$  is very slight. There is a distinct unfavourable effect when the K content exceeds 52 p.p.m., but it is not as pronounced as with *Asterionella*. The influence of different Mg concentrations is approximately the same as in the latter, but the effect of concentrations below 10 p.p.m. is not so deleterious. The optimum concentration of silicate is lower than for the other three diatoms.

*Exp. 17.* The range of suitable concentrations of Ca, Mg, K,  $\text{SiO}_2$  and P as estimated by one month's growth are summarized in Table 22.

Table 22. *Suitable concentrations, in p.p.m., of different salts and elements for the growth of Tabellaria flocculosa*

Salts and elements	Suitable concentration			Usual suitable range
	K <sub>2</sub> HPO <sub>4</sub>	MgSO <sub>4</sub> ·7H <sub>2</sub> O	CaCl <sub>2</sub> ·6H <sub>2</sub> O	
K <sub>2</sub> HPO <sub>4</sub>	1-10	—	—	1-10
MgSO <sub>4</sub> ·7H <sub>2</sub> O	—	10-100	—	10-100
CaCl <sub>2</sub> ·6H <sub>2</sub> O	—	0-500	—	0-500
KCl	—	0-40	—	0-40
K <sub>2</sub> SiO <sub>3</sub>	—	—	5-50	5-50
FeCl <sub>3</sub>	0.84-1.26	—	—	0.84-1.26
P	0.2-1.8	—	—	0.2-1.8
Mg	—	1.9-6	—	1.9-6
Ca	—	10-91	—	10-91
K*	—	13.6-34.5	—	13.6-34.5
SiO <sub>2</sub>	—	—	2-19.6	2-19.6
Fe	0.3-0.4	—	—	0.3-0.4
Media	10	9	6	—

\* See footnote under Table 9 (p. 308).

Media like 10, 12 and 17, in which the concentrations are within the range shown by this experiment, were found to be satisfactory. Medium 17 affords the quickest growth during the first week and in it the filaments are longer than in the others. After 2 weeks the growth in 10 and 12 is better than in 17, while after 6 weeks that in 10 is the best. At the end of 10 weeks both 10 and 12 show a decrease in colour. The growth of *Tabellaria flocculosa*, unlike that of *Asterionella gracillima*, is thus quicker in medium 17 than in 10.

Generally speaking media 9, 10, 12 and 17 are equally suitable for the culture of *Tabellaria flocculosa*, the last in particular affording a vigorous growth in a short time. For cultures of longer duration media 10 and 12 and especially the former are preferable. This diatom grows well on agar (1.5 %) made up with any of the four media.

### 8. *Tabellaria fenestrata*

This diatom, also isolated from Windermere, grows well in media 9 and 10 and also on agar made up with these solutions, though not so rapidly as the diatoms previously studied. The growth in media 9 and 10 is much slower than that of *T. flocculosa*; in 10 the number

of cells in the colonies is greater than in 9. On agar the growth consists of long ribbons with the cells arranged as in *Fragilaria*.

Parallel cultures of *T. fenestrata* in media 11 and 17 afforded better growth in the former, but the growth in both is not as good as in 9 and 10. Though belonging to the same genus, this species seems to differ somewhat from *T. flocculosa* in its requirements.

### 9. *Oscillatoria tenuis* Ag.

*Oscillatoria tenuis*, isolated from Windermere, grew well in media 9 and 10 and very slowly on agar, made up with these media. A number of filaments often project from the main mass and afford good material for isolation.

### 10. *Oscillatoria rubescens* DC.

This blue-green alga, isolated from Sunnyside Reservoir of the Metropolitan Water Board, London, proved very difficult to culture. A large number of media and their modifications were tested. When the suitable range of concentrations of various salts had been obtained in the same way as in earlier experiments, medium 10 was found to contain all the important salts in a suitable concentration. *Oscillatoria rubescens* grows well in this medium.

### 11. *Pandorina morum* (Muell.) Bory, *Euglena deses* Ehrenb., *Lepocinclis Steinii* Lemm., *Cryptomonas ovata* Ehrenb.

*Pandorina morum* is the easiest of these flagellates to culture. It was first raised in Benecke's solution and on agar made up with this solution. It also grows well in all the media 1-17. As in the case of *Botryococcus*, it can stand higher concentrations of nitrogen and phosphorus than the other species considered in this paper. *Cryptomonas ovata* is very difficult to culture and no vigorous growth was obtained before medium 10 was available, though moderate growth was obtained in media 5 and 6. Both *Pandorina* and *Cryptomonas* grow well in medium 10, in which *Euglena deses* and *Lepocinclis Steinii* also flourish.

### SUMMARY

1. Suitable media for the growth of various plankton algae have been prepared using pure chemicals, the formulae being based on the results of series of experiments and on the analyses of fresh waters. In composition and degree of dilution they are comparable with ordinary natural waters, so that experimental results obtained with them should be applicable to natural conditions. Fourteen planktonic algae, isolated from various localities, have been maintained in these solutions in unialgal culture in a flourishing condition for more than two years and could no doubt be cultured indefinitely.

2. The suitable ranges of important salts, liable to change in natural waters, have been determined for the growth of different planktonic algae and the effect on their development discussed.

3. With few exceptions (e.g. *Botryococcus*, which grows better with nitrate N), the planktonic algae investigated grow equally well in media supplied with nitrate and in those supplied with ammonium salts as long as the N concentration is within the optimum range, but in lower N concentrations growth is generally better when nitrate is supplied.

4. The most favourable concentrations of Ca, Mg, K, Na and SiO<sub>2</sub> differ considerably for different algae. Thus *Pediastrum Boryanum* favours low concentrations of Ca, Mg, and SiO<sub>2</sub>, but comparatively higher concentrations of K; diatoms favour high concentra-

tions of Ca, Mg and SiO<sub>2</sub>, and lower concentrations of K; while *Botryococcus* has great tolerance for high Na concentrations.

5. The Ca requirement is often lower in media with higher Mg concentrations, while the presence of excessive K renders the organisms tolerant of higher concentrations of Ca and Mg.

6. No appreciable quantity of SiO<sub>2</sub> is necessary for the growth of planktonic algae, with the exception of diatoms. There is an unfavourable effect on the growth of *Pediastrum* when the SiO<sub>2</sub> concentration exceeds 4 p.p.m. and on *Staurastrum paradoxum* and *Botryococcus* when it is more than 20 p.p.m. The inhibiting effect is marked, even on diatoms, when the concentration is more than 54 p.p.m.

7. The requirements of N and P agree well among the different planktonic algae, in contrast to the requirements of Ca, Mg, K, Na and SiO<sub>2</sub>, though there are minor differences in the lower and upper limits that are suitable. All the algae studied flourish in media with N 1-7, and P 0.1-2 p.p.m., and are likely to suffer from a deficiency when the concentration of N is below 0.2 and that of P below 0.05, and from an inhibiting effect when the concentrations of N and P exceed 20 p.p.m.

8. The optimum range of P concentration is often wider when nitrate is used than when an ammonium salt is used as a source of N.

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## EXPERIMENTS ON THE UTILIZATION OF NITROGEN IN FRESH WATER

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*(With one Figure in the Text)*

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### 1. INTRODUCTION

This investigation was designed as an experimental approach to one aspect of the ecology of fresh-water algae. Previous work on nitrogen utilization in fresh waters has taken the form either of observations on natural bodies of water (Mortimer, 1938), in which any experimental control of conditions is impossible, or of work on algae in the artificial conditions of pure culture (Ludwig, 1938; Pearsall & Loose, 1937). The experiments described in this paper were carried out in a series of tanks, sunk in the ground out-of-doors and covered with glass lids, providing an environment which resembled that of a shallow pond but which could be controlled and altered as desired. The absence of inflow, outflow or bottom mud, though introducing important differences from the pond environment, simplified the interpretation of changes in water composition. One of the chief difficulties in the investigation of nitrogen utilization by algae, under conditions other than those of pure culture, is to differentiate between changes produced by the algae and those produced by bacteria. In the following experiments, no attempt has been made to do this, so that it is impossible to do more than suggest mechanisms to explain the results obtained. Since, however, algae and bacteria always occur together in ponds and lakes, the same difficulty will occur with all results from natural bodies of water.

The results obtained from these experiments were not precisely repeatable; this is what would be expected when the complexity of the ecological system and the impossibility of reproducing conditions exactly are considered. In early experiments, tanks which were given identical treatment showed wide variations in behaviour, and although certain causes of this variation were traced and eliminated (Pennington, 1941) it was still found impossible, over a relatively long period, to obtain closely corresponding results from identically treated tanks. The results discussed here were obtained from such long-period experiments, and in view of the evidence for the development of marked individuality in the behaviour of identically treated tanks, it was not considered profitable to run the experiments in duplicate. In certain cases the results were confirmed by a repetition of the whole experiment at a later date; in others, such a repetition produced different results from the original experiment, presumably because a different system of algae and bacteria

was present. It is believed, however, that these results illustrate the type of ecological changes which occur in natural habitats.

## 2. PLAN OF EXPERIMENT, AND SAMPLING TECHNIQUE

Two types of tank were used: glass battery jars of about 20 l. capacity, and cylindrical vessels of glazed earthenware of about 12 l. capacity. The tanks of each type were covered with glass lids, which prevented dilution of the contents by rain water; beneath these lids evaporation was negligible. The tanks were exposed to full sunlight in open ground. Experiments in 1940 were carried out in the University of Reading Botanic Garden; those in 1941 at Wray Castle. Samples for analysis were withdrawn after thorough stirring of the water, thus ensuring that the sample was representative of the entire contents of the tank. It may be pointed out here that this fact greatly simplified the interpretation of the results, in contrast with the work on natural bodies of water, where it is generally impossible to obtain such a representative sample. The special sampling technique employed in withdrawing samples for determination of dissolved oxygen and redox potential is described in Appendix 1.

## 3. RESULTS

The results from each experiment illustrate several points, and for the sake of clarity the relevant data from the several experiments are grouped together under the appropriate headings. The complete tables of data for each experiment are given in Appendix 2.

The water in the tanks was a rich culture solution, the composition of which is given in Appendix 2. Experiments were carried out using three different sources of nitrogen, viz. ammonium sulphate, ammonium nitrate, and potassium nitrate. Four experiments were carried out on the first two and three on the last.

The flora which developed in the tanks was always of a similar type, consisting practically wholly of members of the Chlorococcales. In all cases where figures are given for parallel experiments in different tanks, the flora of all the tanks was similar; the dominant alga was either *Chlorella*, *Diogenes* (which closely resembles *Chlorella*) or *Scenedesmus*. In bright summer weather the number of algal cells was sometimes very high, reaching 20,000 per cu. mm., but in most of the experiments mentioned here the number was between 200 and 1000 per cu. mm.

### (a) Utilization of nitrogen as ammonia and as nitrate

In water treated with ammonium sulphate, dissolved ammonia decreased fairly rapidly, presumably due to absorption by the algae and bacteria. Where potassium nitrate was the source of nitrogen, dissolved nitrate decreased at a rate rather lower than that at which ammonia decreased from ammonium sulphate, under the same conditions. With ammonium nitrate, the ammonia always decreased before the nitrate, but in a later experiment (May–June 1940), nitrate began to disappear before the ammonia was completely exhausted.

Corresponding with this decrease in ammonia or nitrate nitrogen, there was a steady increase in organic nitrogen as the algal and bacterial population of the tanks increased. It will be observed from the following data that in some cases this increase in organic nitrogen was just sufficient to compensate for the decrease in nitrate or ammonia nitrogen,

*Utilization of nitrogen in fresh water*

so that there was no significant change in the amount of total nitrogen; in other experiments a marked decrease in total nitrogen took place. This will be discussed in more detail under a separate heading.

Table 1.\* *Results for experiment of February–May 1940*

## (a) Ammonium sulphate

	Ammonia N
Added—9 Feb.	70·7
Estimated—12 Mar.	66·0, 62·0
Estimated—7 May	49·5, 49·4

## (b) Ammonium nitrate

	Ammonia N	Nitrate N
Added—9 Feb.	19·8	19·8
Estimated—12 Mar.	17·6, 17·8	21·6
Estimated—7 May	10·6, 10·2	19·0, 20·9
Estimated—21 May	4·7, 5·1	21·3, 24·5

## (c) Potassium nitrate

	Nitrate N
Added—9 Feb.	50·1
Estimated—12 Mar.	47·9, 46·0
Estimated—7 May	34·2, 35·7

*Results for experiment of May–June 1940*

## (a) Ammonium sulphate

	Ammonia N
Added—8 May	76·7
Estimated—5 June	14·0, 14·8

## (b) Ammonium nitrate

	Ammonia N	Nitrate N
Added—8 May	17·2	17·2
Estimated—5 June	5·9, 6·3	8·5, 7·8

## (c) Potassium nitrate

	Nitrate N
Added—8 May	50·2
Estimated—5 June	29·6, 27·5

\* In all tables, two results separated by a comma, or bracketed, indicate duplicate estimations.  
All results are in mg./l.

Table 2. *Experiment of February–May 1940*

## (a) Ammonium sulphate

	Ammonia N	Nitrate N	Organic N	Total N
Added—9 Feb.	70·7	0	0	70·7
Estimated—7 May	49·5	3·5	8·3	61·3

## (b) Ammonium nitrate

Added—9 Feb.	19·8	19·8	0	39·6
Estimated—21 May	4·7, 5·1	21·3, 24·5	11·9, 6·3	37·9, 35·9

## (c) Potassium nitrate

Added—9 Feb.	0	50·1	0	50·1
Estimated—7 May	1·3, 1·2	34·2, 35·7	7·5, 7·3	43·0, 44·2

*Experiment of August–September 1941*

## (a) Ammonium sulphate

	Ammonia N	Nitrate N	Organic N	Total N
Added—8 Aug.	65·0	0	0·5	65·5
Estimated—5 Sept.	56·1, 59·5	0·8, 0·7	5·4, 3·4	62·3, 63·6

## (b) Ammonium nitrate

Added—8 Aug.	26·3	26·3	0·5	53·1
Estimated—6 Sept.	17·3, 23·6	27·5, 28·8	4·5, 7·2	49·3, 59·6

By removing the algae and most of the bacteria by precipitation with aluminium sulphate, and carrying out a Kjeldahl estimation on the filtrate, it was proved that part

of the organic nitrogen produced was in soluble form, but no determinations of its nature were carried out.

The results given so far were all obtained under aerobic conditions. In two experiments, water treated with ammonium nitrate was made anaerobic by the addition of 2 g./l. of glucose. This stimulated both algal and bacterial reproduction, and within a few days conditions favourable to reduction appeared as a result of the great increase in bacterial activity. Under these conditions, nitrate disappeared completely from the water, and ammonia decreased very rapidly. This suggests that nitrate was rapidly reduced and ammonia was rapidly utilized by the increasing algal and bacterial population. In water treated with ammonium sulphate, when anaerobic conditions were produced in the same way, there was a similar rapid decrease in dissolved ammonia, corresponding with a rapid increase in the population of algae and bacteria.

Table 3. *Experiment of August–September 1941*

(a) Ammonium nitrate

	Ammonia N	Devarda N	Nitrate N (col.)	Organic N	Dissolved O <sub>2</sub>
Added—8 Aug.	26.25	26.25	—	0.5	—
Glucose added—28 Aug.	—	—	—	—	10.8
Estimated—6 Sept.	2.1, 0.77	2.0, 2.0	0.0	45.9, 44.8	0.3

(b) Ammonium sulphate

	Ammonia N	Organic N	Dissolved O <sub>2</sub>
Added—8 Aug.	64.6	0.5	14.8
Glucose added—28 Aug.	—	—	—
Estimated—5 Sept.	24.4, 23.4	44.9	0.2
Estimated—11 Sept.	17.9, 18.3	51.7	—
Estimated—22 Sept.	1.3, 1.2	64.5, 61.6	—

(b) *Interconversion of forms of nitrogen*

(i) *Aerobically*

*Nitrite*, though not originally present in any tank, was found in all within the space of a week or two, irrespective of whether nitrogen had been added as ammonia or nitrate, or both. It was found in greatest quantity where the concentration of nitrate was highest—that is, in the tanks treated with potassium nitrate, and in traces only in the tanks treated with ammonium sulphate. This suggests that nitrite was formed most readily as a result of reduction of nitrate. When aerobic conditions were maintained throughout, the amount of nitrite present usually increased slowly throughout the duration of the experiment.

Table 4. *Experiment of February–May 1940*

Chemical treatment

Date	Ammonium sulphate		Ammonium nitrate	Potassium nitrate
	Nitrite N	Nitrite N	Nitrite N	Nitrite N
9 Feb.	0	—	0	0
26 Mar.	0.05	—	0.1	0.1
21 May	0.6	—	3.3	5.0

*Interconversion of ammonia and nitrate.* In tanks treated with potassium nitrate having initially no ammonia, small quantities of ammonia nitrogen shortly appeared, i.e. ammonia was evolved when the water was distilled with potassium bicarbonate. This almost certainly represents free ammonium salts, not amide nitrogen, since the evolution of ammonia on distillation occurred rapidly and then ceased. It is therefore suggested that production of small quantities of ammonia occurs in water treated with nitrate.

## *Utilization of nitrogen in fresh water*

In the later stages of the long-term experiments there is evidence that small quantities of nitrate appear in water treated with ammonium sulphate. Samples of the water were first distilled with potassium bicarbonate to remove the ammonia, and then reduced with Devarda alloy plus strong alkali. Small quantities of ammonia were given off.

It must be admitted that these figures do not prove the existence of nitrate conclusively. In certain experiments it was found that some of the Devarda nitrogen was evolved in the presence of strong alkali only by the action of this on the organic nitrogenous compounds; this occurred in both oxidizing and reducing waters, particularly in the presence of large quantities of organic nitrogen (see Table 6). In low concentrations of organic nitrogen such as were found in the experiment given in Table 5*b* (4-5 mg./l.), the amounts of nitrogen evolved in this way were very small, so it is almost certain that part at least of 2.3 mg./l. of Devarda nitrogen evolved was derived from nitrate.

Table 5*a*. *Experiment of February–May 1940*

Potassium nitrate	Ammonia N	Nitrate N
Added—9 Feb.	0	50.1
Estimated—1 Apr.	0.5, 0.4	35.5, 36.4
Estimated—7 May	1.3, 1.2	34.2, 35.7

Table 5*b*. *Experiment of February–May 1940*

Ammonium sulphate	Devara N	Ammonia N	Organic N
Added—9 Feb.	0	70.7	0
Estimated—9 Apr.	2.3, 2.3	60.5, 59.0	4.9, 4.1

Table 6. *Experiment of August–September 1941*

(a) Ammonium nitrate  
1. Oxidizing

	Ammonia N	D.1	D.2	Nitrate N (col.)	Organic N
Added—6 Aug.	26.2	26.2	26.2	—	0.5
Estimated—6 Sept.	17.3, 23.6	0.5, 0.2	27.1, 28.6	22.5	4.5, 7.3
2. Reducing					
Added as above					
Estimated—6 Sept.	2.1, 0.8	1.8, 2.0	0.01, 0.04	0	45.9, 44.8

D.1—Fraction evolved with strong alkali only.

D.2—Fraction evolved when Devarda alloy added to strong alkali.

It was not possible to confirm the presence of nitrate by the colorimetric phenol-disulphonic acid method because of the presence of soluble organic matter which produced a brown colour with the acid.

(ii) *Anaerobically*

Fig. 1 illustrates the changes in ammonia, nitrate and nitrite which were observed in a tank treated with ammonium nitrate, in which anaerobic conditions were produced by adding glucose as already described. After the addition of the glucose, the changes in redox potential at pH 7 (*E*7),<sup>1</sup> and amounts of nitrate, nitrite, and dissolved oxygen were determined daily, and the results, given in Appendix 2, show an interesting relation between these variables. Nitrate, estimated by the phenol-disulphonic colorimetric method,

<sup>1</sup> For a discussion of the theory and significance of redox potentials, see Pearsall (1938), and Pearsall & Mortimer (1939).

began to decrease on the day after the  $E_7$  had fallen below 200 mV., and continued to decrease steadily for four days, after which nitrate completely disappeared; on the following day the tank was almost completely anaerobic, with a very low redox potential. This agrees well with results observed in the field by Pearsall & Mortimer (1939). They found that in Blelham Tarn, Lancashire, nitrate was not found in water with a potential equivalent to less than 234 mV. at pH 7.

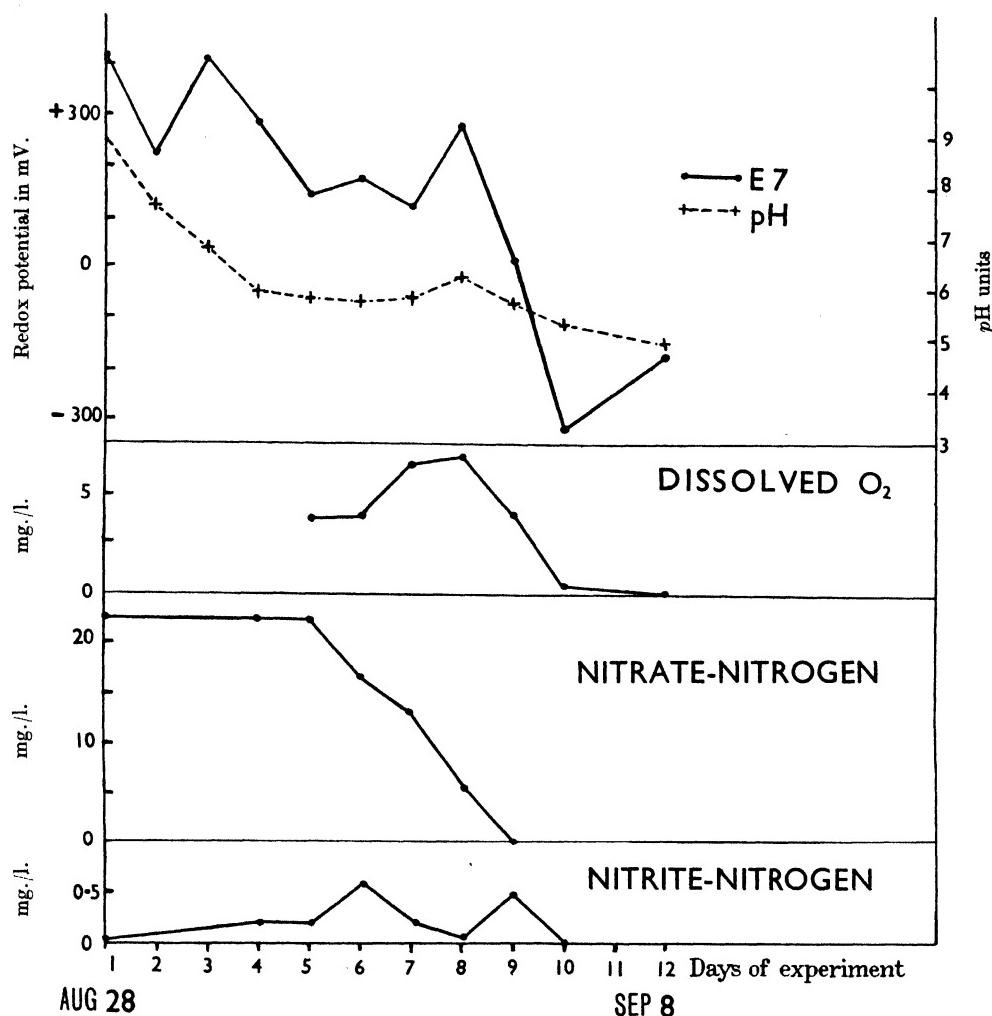


Fig. 1. Changes in redox potential, pH, dissolved oxygen, nitrate nitrogen and nitrite nitrogen, in a tank treated with ammonium nitrate to which 2.5 g./l. glucose was added on 28 August.

Nitrite in this tank increased as the redox potential first began to fall, presumably due to reduction of nitrate, but as the water became increasingly depleted of oxygen, nitrite decreased, and disappeared on the day after the disappearance of nitrate. An estimation of total nitrogen made on the same day showed that ammonia had almost completely disappeared, and that organic nitrogen had greatly increased. This corresponds with the great increase in the numbers of algae and bacteria which followed the addition of glucose.

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In this estimation, the 2 mg./l. of nitrogen produced by the Devarda reduction were all evolved with alkali only, and were therefore derived entirely from organic compounds of nitrogen.

Table 7. *Experiment of August–September 1941*

	Ammonia N	Devarda N	Nitrite N (col.)	Nitrate N (col.)	Organic N	Dissolved O <sub>2</sub>	E 7
28 Aug. (glucose added)	19.5, 24.3	27.4, 26.5	0.025	22.5	3.0, 5.5	10.8	414
2 Sept.	—	—	0.6	16.9	—	3.9	180
5 Sept.	—	—	0.5	0	—	4.0	17
6 Sept.	2.1, 0.8	1.8, 2.0	0	—	45.9, 44.8	0.3	-323

(c) *Loss of nitrogen*

In some of the experiments, the figures for total nitrogen (the sum of ammonia nitrogen, Devarda nitrogen, and organic nitrogen) indicate that there was an appreciable loss of nitrogen from the water during the experiment. Under aerobic conditions, a marked loss of nitrogen was observed on three occasions from tanks treated with ammonium sulphate and potassium nitrate respectively, though in a later experiment with ammonium sulphate there was no such loss. From ammonium nitrate under aerobic conditions, no significant decrease in total nitrogen was ever observed; in an anaerobic tank, there was in one experiment a marked loss of nitrogen from ammonium nitrate, but in another experiment this did not occur.

Table 8. *Experiments of February–May 1940*

## Aerobic conditions

	Ammonium sulphate Total N	Potassium nitrate Total N
1. Added—9 Feb.	70.7	50.1
Estimated—3 Mar.	51.6, 51.6	45.2, 39.3
Loss of nitrogen	19.1/70.7 = 27 %	7.8/50.1 = 16 %
2. Added—9 Feb.	70.7	50.1
Estimated—21 May	59.1	43.0, 44.2
Loss of nitrogen	10/70 = 14 %	6.5/50 = 13 %

*Experiment of May–June 1940*

	Ammonium sulphate	Potassium nitrate
Added—8 May	76.7	50.2
Estimated—5 June	24.8, 29.9	43.5
Loss of nitrogen	49/77 = 64 %	7/43 = 16 %

*Experiment of June 1940*

## Anaerobic conditions

	Ammonium nitrate Total N
Estimated—6 June	73.3
Estimated—18 June	57.4
Loss of nitrogen	16/73 = 22 %

It appears from these results that a marked loss of nitrogen may occur from water heavily dosed with nitrate or ammonia in which algae and bacteria are growing, but that not all the algal-bacterial systems commonly found in fresh water are capable of producing this loss of nitrogen. It is easy to see how this loss could occur, through the effect of denitrifying bacteria on nitrates, and the presence of such bacteria was demonstrated in the tank manured with potassium nitrate, the results from which are given in Table 8. The loss of nitrogen from ammonium sulphate was more difficult to explain; it was just

possible that ammonia was given off from the surface of the water, which was alkaline ( $\text{pH } 7.5-9.0$ ). A sample of the water was kept in a darkened glass bottle, and ammonia-free air bubbled through it each day for a month, the air then being passed through dilute acid; the amount of ammonia given off during the month was negligible. Some biological mechanism is therefore involved in the loss of nitrogen from ammonium sulphate. Possible mechanisms are discussed later.

#### 4. DISCUSSION

The rapid decrease in dissolved ammonia and nitrate was presumably due to utilization by algae and bacteria. These experiments do not, of course, show in which form nitrogen was actually absorbed by the living organisms, but the results suggest that ammonia was absorbed in preference to nitrate. In water treated with ammonium nitrate, ammonia always decreased fairly rapidly for some time before the nitrate began to decrease, and in water treated with ammonium sulphate, ammonia decreased rather more rapidly than did nitrate from water treated with potassium nitrate. This preferential absorption of ammonia agrees with the results obtained by workers on the Chlorophyceae in pure culture. Ludwig (1938), working on the nitrogen uptake of *Chlorella* and other unicellular green algae, found that more nitrogen was absorbed as ammonia nitrogen, from inorganic salts of ammonia, than was absorbed as nitrate nitrogen from nitrates. Pearsall & Loose (1937) found that *Chlorella* in pure culture in ammonium nitrate absorbed ammonia more rapidly than nitrate.

It has been suggested in the previous section that these experiments indicate the production of nitrate from ammonia, ammonia from nitrate, and nitrite from both ammonia and nitrate. The test for nitrite is probably reliable, but the lack of satisfactory methods for estimating small quantities of ammonia and nitrate in the presence of large quantities of organic matter means that it is not possible to say with complete certainty that these were produced. The results suggest, however, that ammonia is produced from nitrate and nitrite from ammonia, under similar conditions; this indicates the presence of living systems similar to those found in soil (Russell, 1937), capable of oxidizing and reducing nitrogen compounds.

The ecological importance of this is that, since under the conditions prevailing in the tanks (which are in many respects similar to those of alkaline ponds), nitrate may be produced from ammonia and ammonia from nitrate, it appears to be immaterial to the flora in which form nitrogen is added to the water. It would also explain the similarity of the flora in tanks manured with ammonia only, with nitrate only, and with both ammonia and nitrate.

Under anaerobic conditions, the results obtained were rather different. It is realized, however, that the addition of glucose to produce anaerobiosis must have introduced additional complications. Bacteria and algae both increased in numbers, particularly the bacteria, whose increased activity led to the development of anaerobic conditions; the normal balance of the ecological system would therefore be disturbed. Nevertheless, these experiments indicated that as the redox potential fell, nitrate decreased in amount, and disappeared at  $E 7.200$  to  $250 \text{ mV.}$ , which approximates to the potential found by workers in the field to be that at which nitrate disappears (Pearsall & Mortimer, 1939). The great increase in organic production in the water, leading to very rapid decrease in ammonia, meant that it was not discovered whether this nitrate was converted into

ammonia, or seized upon and utilized by bacteria and algae during the reduction. The increase in nitrite in the early stages of nitrate reduction is significant.

One of the most interesting results of these experiments was the marked decrease in total nitrogen which sometimes occurred. This indicates a loss of nitrogen, presumably as free nitrogen. Since there is no inflow or outflow, the only other possible means of escape of nitrogen from the water would seem to be the escape of mature insects which had fed as larvae in the water. Estimations of the nitrogen content of insect larvae in the tanks had shown that this loss would be relatively very small; in most of the experiments quoted here, no such loss could occur, because the tanks were covered with glass lids.

Assuming that loss of nitrogen as free nitrogen took place, this presumably resulted from the activities of bacteria, or algae, or both. The conditions governing this loss are still unknown; it would therefore be useless to discuss possible causes at any length. Two possible mechanisms are known; first, loss of nitrogen during algal metabolism (see, for example, Pearsall & Loose, 1937; Pearsall & Billimoria, 1937), and secondly denitrification by bacteria (reduction of nitrate with production of free nitrogen) (see Waksman, 1932; Meiklejohn, 1940).

Pearsall and his fellow workers found that there was loss of nitrogen from pure cultures of *Chlorella* supplied with ammonium nitrate. The loss is supposed to result from the reaction of nitrite, if present as nitrous acid, with mono-amino nitrogen. Nitrite was present in the water of all tanks, and though the water was too alkaline for the above reaction to take place, it is possible that it occurred in the interior of the living cells, where the pH was probably between 5.0 and 6.0 (Pearsall & Billimoria, 1937). In many tanks where algal growth became abundant, there was no appreciable loss of nitrogen, while in other experiments there was a considerable nitrogen loss from water containing only a few algae. This suggests that bacteria rather than algae were mainly responsible for the loss. Bacteria capable of liberating nitrogen from nitrate were found in certain tanks. If, as the evidence suggests, nitrate was formed in tanks originally treated with ammonium sulphate but no nitrate, bacterial reduction of nitrate may explain the losses of nitrogen from such tanks as well as from tanks treated with nitrate. No attempt was made to investigate further the distribution of these bacteria in the tanks. It seems likely that they may have been present only in those tanks where nitrogen loss occurred; this subject appears a promising one for further work.

Whatever the mechanism of the nitrogen loss, its ecological significance is obvious. If loss of nitrogen occurs from a pond or lake, by denitrification or during the metabolism of green algae, it would be an important factor in the chemical cycle and in the history of the lake. Mortimer (1938) has shown that in the annual 'nitrogen budget' of Windermere such a loss apparently occurs, but in the presence of a mud system with possibilities of exchange of ions between mud and water, it is not possible to ascribe that loss with any certainty to loss of free nitrogen due to the activities of bacteria or algae.

##### 5. SUMMARY

The experiments described were carried out on mixed cultures of algae and bacteria, in a rich culture solution containing nitrate or ammonia; conditions were in many respects similar to those found in lowland ponds, though the culture solution was richer than most pond waters.

Ammonia and nitrate were both utilized, but ammonia appeared to be used more rapidly.

Nitrite was produced from both ammonia and nitrate; there is evidence that ammonia was produced from nitrate and nitrate from ammonia.

In some experiments there was a marked loss of nitrogen from the cultures, apparently indicating liberation of gaseous nitrogen.

I wish to thank Prof. T. M. Harris for help and criticism throughout this work, and Dr C. H. Mortimer for valuable discussion and advice on chemical methods. Most of the experiments described in this and a preceding paper (Pennington, 1941) were carried out during the tenure of a Maintenance Allowance from the Department of Scientific and Industrial Research, and a Senior Scholarship of Reading University; grateful acknowledgement is made to both these bodies.

#### APPENDIX 1. METHODS OF CHEMICAL ANALYSIS

##### (a) *Estimation of total nitrogen*

Total nitrogen was estimated as the sum of ammonia nitrogen, Devarda nitrogen, and Kjeldahl nitrogen. These were estimated on the same sample. For further discussion of this method, see Corbet & Wooldridge (1940).

A 100 c.c. sample was used. Approximately 2 g. of potassium bicarbonate were added, and the sample distilled in a flask with a steam trap. The ammonia evolved was collected in *N*/20 standard acid, unless only minute amounts were present; these were collected in ammonia-free water and Nesslerized. The distillation was continued until two-thirds of the sample had distilled over.

15 c.c. of 50 % potassium hydroxide and 1 g. of powdered Devarda alloy were then added to the residue, the neck of the flask was plugged with glass-wool, and the receiving vessel put in position. As above, the ammonia evolved was collected in standard acid or in ammonia-free water for Nesslerization, according to the amount present. The flask was gently warmed for 1 hr., and the ammonia formed by reduction of nitrite and nitrate was then distilled over.

A Kjeldahl estimation of organic nitrogen was then carried out on the residue in the flask.

##### (b) *Colorimetric estimation of nitrite and nitrate*

These were carried out by the standard methods (see American Public Health Assoc. 1936). Nitrite was estimated by the method of Griess-Ilosvay; nitrate by the phenol-disulphonic acid method.

##### (c) *Estimation of dissolved oxygen*

Dissolved oxygen was estimated by the standard Winkler method (see American Public Health Assoc. 1936, unless large quantities of organic matter were present, in which case the modified technique of Alsterberg, described by Ohle (1936) was used).

The samples were withdrawn from the tank in such a manner that they did not come into contact with air. A flask of 100–150 c.c. capacity was introduced into the tank, and a current of tank water was drawn through it, using a bicycle pump and a large bottle. When 300 c.c. of tank water had been drawn into the bottle, the flask was stoppered under water, so that no air bubbles were included. The contents of the large bottles were then returned to the tank, thus avoiding undue decrease in volume of contents.

(d) *Determination of redox potential*

This was determined by the apparatus described by Pearsall & Mortimer (1939). Samples were withdrawn by the method used for samples for dissolved oxygen.

## APPENDIX 2. COMPLETE DATA FROM EXPERIMENTS

(As mg./l. unless otherwise stated)

1. *Experiment of February–March 1940*

## (a) Ammonium sulphate

	Added						
Date	... 9. ii	12. ii	16. ii	21. ii	26. ii	4. iii	12. iii
Ammonia N	70.7	{64.9 71.7	{64.8 64.1	{60.8 —	{58.5 58.5	{49.1 51.8	{49.5 50.5
Kjeldahl N	0	{0.8 1.6	{0.45 0.5	{1.2 —	{0.6 0.6	{0.6 0.6	{2.1 1.1
Total N	70.7	{65.7 73.4	{65.3 64.6	{62.0 —	{59.1 59.1	{49.7 52.2	{51.6 51.6
Nitrite N (col.)	—	—	—	0.6	0.3	0.3	—
E7 in mV.	—	467	—	447	456	403	—
O <sub>2</sub> % sat.	—	45	—	38	57	40	—
Algae per cu.mm.	—	11	22	14	18	17	96

## (b) Potassium nitrate

	Added						
Date	... 9. ii	12. ii	16. ii	21. ii	26. ii	4. iii	12. iii
Ammonia N	0	0	0	0	0	0	Trace
Devarda N	50	{53 43	{46 49	{45 51	{41 35	{45 39	—
Kjeldahl N	0	{0.45 0.45	{0.2 0.2	{0.6 0.6	{0.6 0.6	{0.2 0.3	—
Total N	50	{53.45 43.45	{46.2 49.2	{45.6 51.6	{41.6 35.6	{45.2 39.3	—
Nitrate N (col.)	—	{51 59	{64 70	{51 49	{59 58	—	—
Nitrite N (col.)	—	—	0.76	3.0	6.2	—	—
E7 in mV.	—	—	457	424	513	—	—
O <sub>2</sub> % sat.	—	—	49	57	—	—	—
Algae per cu.mm.	—	14	12	14	29	867	—

## (c) Ammonium nitrate

	Added						
Date	... 9. ii	12. ii	16. ii	21. ii	26. ii	4. iii	12. iii
Ammonia N	19.8	{17.7 18.0	{15.9 16.8	{18.1 15.7	{14.3 15.0	{10.2 10.2	—
Devarda N	19.8	{18.4 20.7	{16.5 19.0	{22.3 21.6	{17.8 18.5	{19.3 25.6	—
Kjeldahl N	0	{0.3 0.7	{0.4 0.08	{0.6 0.7	{0.6 0.6	{2.4 0.9	—
Total N	39.6	{36.4 39.4	{32.8 35.9	{41.0 38.0	{32.7 34.1	{31.9 36.7	—
Nitrate N (col.)	—	{24.2 25.3	{24.0 23.0	{22.6 22.6	{18.8 18.8	—	—
Nitrite N (col.)	—	0	0.4	0.8	1.5	—	—
E7 in mV.	—	398	483	471	464	—	—
O <sub>2</sub> % sat.	—	73	64	64	74	—	—
Algae per cu.mm.	—	16	17	11	16	31	—

## 2. Experiment of February–May 1940

## (a) Ammonium sulphate added

Date	9. ii	12. iii	18. iii	26. iii	1. iv	9. iv	24. iv	7. v	21. v
Ammonia N	70.7	{66.0 62.0	{62.8 63.6	{63.0 60.6	{59.3 60.6	{60.5 59.0	{50.2 56.0	{49.5 49.4	{36.2 41.5
Devarda N	0	—	—	—	{2.8 5.4	{2.3 2.3	{3.6 7.0	{3.5 —	{4.2 —
Kjeldahl N	0	{1.2 1.2	{2.6 2.2	{6.2 7.3	{4.6 4.6	{4.9 4.1	{3.6 7.0	{8.2 —	{11.3 13.4
Total N	70.7	{67.2 63.2	{65.4 65.8	{69.2 67.9	{66.7 70.6	{67.7 65.4	{57.4 66.6	{61.3 —	{— 59.1
Nitrite N (col.)	—	—	0.15	0.05	0.06	0.18	0.2	0.8	0.6
E7 in mV.	—	516	510	416	483	472	434	431	430
O <sub>2</sub> % sat.	—	83	170	170	180	121	94	115	116
Algae per cu.mm.	—	46	296	1236	2328	1454	1200	628	2083

## (b) Potassium nitrate added

Date	9. ii	12. iii	18. iii	26. iii	1. iv	9. iv	24. iv	7. v	21. v
Ammonia N	0	Trace	{3.3 2.3	{0.7 0.3	{0.5 0.4	{0.7 0.6	{1.5 1.5	{1.3 1.2	{1.6 1.5
Devarda N	50.1	{47.9 46.0	{55.6 53.5	{37.5 43.1	{35.5 36.4	{32.5 42.5	{40.0 41.8	{34.2 35.7	{38.1 32.8
Kjeldahl N	0	{0.9 0.8	{0.8 1.2	{2.8 3.0	{3.7 2.0	{5.0 5.4	{4.1 5.0	{7.5 7.3	{3.6 —
Total N	50.1	{48.8 46.8	{59.7 57.0	{41.0 46.4	{39.7 38.8	{38.2 48.5	{45.6 48.3	{43.0 44.2	{43.3 —
Nitrate N (col.)	—	{70.5 70.4	{59.5 —	{59.4 62.0	{59.3 50.0	{45.0 47.0	{36.7 38.1	{36.5 34.2	{23.2 19.8
Nitrite N (col.)	—	0.3	0.1	0.1	0.08	0.1	0.2	3.6	5.0
E7 in mV.	—	440	520	463	499	494	502	430	524
O <sub>2</sub> % sat.	—	150	160	220	160	170	112	113	127
Algae per cu.mm.	—	241	68	412	825	608	1250	594	5583

## (c) Ammonium nitrate added

Date	9. ii	12. iii	18. iii	26. iii	1. iv	9. iv	24. iv	7. v	21. v
Ammonia N	19.8	{17.6 17.8	{17.0 —	{19.1 18.2	{17.8 —	{15.4 13.0	{14.9 12.3	{10.6 11.2	{4.7 5.1
Devarda N	19.8	{21.6 30.7	{23.0 24.0	{23.1 24.0	{17.3 21.7	{27.0 22.8	{24.4 23.4	{19.0 20.9	{21.3 24.5
Kjeldahl N	0	{0.7 0.8	{1.0 —	{1.2 1.0	{2.1 2.1	{3.7 3.3	{3.3 5.8	{7.3 —	{11.9 6.3
Total N	39.6	{39.9 49.3	{41.0 —	{43.4 43.2	{37.2 —	{46.1 39.1	{42.6 41.5	{36.9 —	{37.9 35.9
Nitrate N (col.)	—	{23.1 —	{20.5 21.6	{23.5 23.5	{25.0 24.5	{23.5 22.5	{24.1 23.1	{21.3 —	{14.9 16.1
Nitrite N (col.)	—	0.15	0.15	0.1	0.06	0.05	0.06	1.0	3.3
E7 in mV.	—	484	490	496	476	484	382	470	439
O <sub>2</sub> % sat.	—	75	85	109	180	157	123	119	134
Algae per cu.mm.	—	43	24	63	652	1000	1590	1085	7250

## 3. Experiment of May–June 1940

	Ammonium sulphate		Potassium nitrate		Ammonium nitrate	
	Added 8 May	Estimated 5 June	Added 8 May	Estimated 5 June	Added 8 May	Estimated 5 June
Ammonia N	76.7	14.0, 14.8	0	1.6, 1.1	17.2	5.9, 6.3
Devarda N	0	3.1, 2.8	50.2	29.6, 27.5	17.2	8.5, 7.8
Kjeldahl N	0	11.3, 12.3	0	12.3, —	0	18.4, 20.5
Total N	76.7	24.8, 29.9	50.2	43.5, —	34.4	32.8, 34.6
Nitrate N (col.)	—	—	—	23.0, 25.6	—	1.6, 2.0
Nitrite N	—	0.55	—	2.0	—	0.4

## 4. Experiment of June 1940

## (a) Aerobic tank

Date	E 7 in mV.	Dissolved O <sub>2</sub> mg./l.	pH	<i>Scenedesmus</i>		Devarda N	Kjeldahl N	Total N	Nitrate N (col.)	Nitrite N (col.)
				nos. per cu.mm.	Ammonia N					
3 June	—	—	—	7,250	—	{21.1 22.6	{25.8 26.7	{— 24.0	{— 73.3	{28.3 26.2
6 „	—	—	—	—	—	—	—	—	—	0.4
12 „	392	—	9.3	—	—	—	—	—	—	—
13 „	410	—	9.2	—	{19.5 19.5	{19.6 —	{27.0 29.7	{66.1 —	{19.8 19.8	0.8
16 „	407	14.4	9.3	—	—	—	—	—	—	—
17 „	379	7.0	9.3	11,750	—	—	—	—	—	—
18 „	376	11.4	9.2	—	{16.4 19.2	{17.2 23.5	{34.2 32.0	{68.8 74.7	{25.5 25.5	2.0
19 „	375	—	9.3	—	—	—	—	—	—	—
20 „	377	11.2	9.3	—	—	—	—	—	—	—
24 „	364	8.6	9.2	17,500	—	—	—	—	—	—

## (b) Anaerobic tank

Date	E 7 in mV.	Dis- solved O <sub>2</sub> mg./l.	pH	<i>Scenedesmus</i>		Devarda N	Kjeldahl N	Total N	Nitrate N (col.)	Nitrite N
				nos. per cu.mm.	Ammonia N					
3 June	—	—	—	7,250	—	—	—	—	—	—
6 „	—	—	—	—	{21.1 22.6	{25.8 26.7	{— 24.0	{— 73.3	{28.3 26.2	0.4
12 „	413	—	9.0	—	—	—	—	—	—	—
13 „	457	--	8.9	—	{18.0 17.5	{22.1 21.8	{31.0 28.3	{71.1 67.6	{17.4 17.4	0.8
16 „	411	0.0	6.8	—	—	—	—	—	—	—
17 „	93	2.3	6.8	15,250	—	—	—	—	—	—
18 „	144	0.0	6.7	—	{3.9 4.2	{5.6 5.7	{— 47.5	{— 57.4	{2.3 2.0	0.2
19 „	204	—	6.8	—	—	—	—	—	—	—
20 „	190	—	6.4	—	—	—	—	—	—	—
21 „	88	—	5.2	—	—	—	—	—	—	—
22 „	-133	—	5.4	—	—	—	—	—	—	—
24 „	-135	0.0	5.1	7,500	—	—	—	—	—	—

## 5. Experiment of August-September 1941

## (a) Ammonium sulphate

Date	pH	E 7	O <sub>2</sub> mg./l.	<i>Chlorella</i>		Ammonia N	Devarda N	Kjeldahl N	Total N
				per cu.mm.	Col. N <sub>3</sub> N Col. N <sub>2</sub> N				
8 Aug.	—	—	—	—	—	65.0	0	0.5	65.5*
	—	—	—	—	—	64.6	0	0.5	65.1†
28 „	8.8	400	—	324	0	0	{49.2 53.0	{2.1 0.3	{54.55 53.99
31 „	8.8	408	—	434	0.1	0.006	—	—	—
1 Sept.	8.6	414	10.0	201	—	0	—	—	—
2 „	8.4	425	10.6	298	0.1	0	—	—	—
3 „	8.3	435	12.3	—	—	0.001	—	—	—
4 „	8.5	258	12.4	526	—	—	{56.1 59.5	{0.7 0.7	{54.3 53.5
5 „	8.4	368	10.2	—	—	—	—	—	63.6

\* Estimated.

† Calculated from addition.

## Anaerobic tank

Date	pH	E7	O <sub>2</sub> mg./l.	Chlorella per cu.mm.	NO <sub>3</sub> N col.	NO <sub>2</sub> N col.	Ammonia N	Devarda N	Kjeldahl N	Total N
8 Aug.	—	—	—	—	—	—	65.0	0	0.5	65.5*
—	—	—	—	—	—	—	64.6	—	0.5	65.1†
28 „	8.8	406	14.8	328	—	—	—	—	—	—
(30 g. glucose added)										
31 Aug.	6.0	296	—	3450	0	0.025	—	—	—	—
1 Sept.	5.6	-211	4.06	2860	—	0.04	—	—	—	—
2 „	5.6	99	2.98	5040	Too organic	0	—	—	—	—
3 „	5.4	-303	2.1	—	—	0	—	—	—	—
4 „	5.2	-19	0.4	4520	—	—	—	—	—	—
5 „	5.0	-76	0.2	—	—	—	{24.4 23.4	{0.17 0.05	{44.95 —	{69.51 —
6 „	5.0	130	0	—	—	0.02	—	—	—	—
11 „	—	—	—	Brown foul	—	—	{17.94 18.3	—	{51.7 —	{70.0 —
22 „	—	—	—	Algal cells dead	—	—	{1.3 1.2	—	{64.45 61.6	{65.75 62.8

## (b) Ammonium nitrate

## Aerobic tank

Date	pH	E7	O <sub>2</sub> mg./l.	Chlorella per cu.mm.	NO <sub>3</sub> N col.	NO <sub>2</sub> N col.	Ammonia N	Devarda N	Kjeldahl N	Total N
8 Aug.	—	—	—	—	—	—	28.8	29.4	0.5	58.7*
—	—	—	—	—	—	—	26.25	26.25	0.5	52.75†
28 „	9.0	424	—	312	22.5	0.025	{19.5 24.3	{27.4 26.5	{3.0 5.5	{49.9 56.3
31 „	9.0	530	—	576	22.5	0.035	—	—	—	—
1 Sept.	8.9	405	10.6	282	22.5	0.035	—	—	—	—
2 „	8.8	414	10.8	578	22.5	0.03	—	—	—	—
3 „	8.9	420	11.5	—	22.5	0.03	—	—	—	—
4 „	8.9	400	11.2	416	22.5	0.04	—	—	—	—
5 „	8.8	455	10.3	—	22.5	0.04	—	—	—	—
6 „	8.8	454	13.2	—	—	0.05	{17.3 23.6	{27.5 28.8	{4.5 7.3	{49.3 59.6

## Anaerobic tank

Date	pH	E7 mV.	O <sub>2</sub> mg./l.	Chlorella per cu.mm.	NO <sub>3</sub> N col.	NO <sub>2</sub> N col.	Ammonia N	Devarda N	Kjeldahl N	Total N
8 Aug.	—	—	—	—	Estimated	—	28.8	29.4	0.5	58.2
—	—	—	—	Calculated from addition	—	—	26.25	26.25	0.5	52.8
28 „	9.0	414	10.8	409	—	—	—	—	—	—
(30 g. glucose added)										
30 Aug.	6.9	414	—	2,050	—	—	—	—	—	—
31 „	6.0	282	—	3,620	22.5	0.2	—	—	—	—
1 Sept.	5.9	146	3.75	4,000	22.5	0.2	—	—	—	—
2 „	5.8	180	3.9	5,320	16.9	0.6	—	—	—	—
3 „	5.9	120	6.4	—	13.2	0.2	—	—	—	—
4 „	6.3	283	6.95	10,920	5.6	0.06	—	—	—	—
(10 g. glucose added)										
5 Sept.	5.8	17	4.0	—	0	0.5	—	—	—	—
6 „	5.4	-323	0.3	—	—	0	{2.1 0.8	{2.0 2.0	{45.9 44.8	{49.8 47.5

\* Estimated.

† Calculated from addition.

*Utilization of nitrogen in fresh water**Composition of the culture solution in the experimental tanks*

All the tanks contained the following salts:

Calcium carbonate,	0·1 g./l.	Potassium sulphate,	0·05 g./l.
Calcium phosphate,	0·05 g./l.	Magnesium sulphate,	0·05 g./l.

In addition, each tank contained *one* of the following sources of nitrogen: ammonium sulphate, potassium nitrate, ammonium nitrate.

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## THE ALGAE OF MILES ROUGH BOG, BRADFORD

By A. MALINS SMITH

(With one Figure in the Text)

Algae were collected from Miles Rough bog at approximately monthly intervals from March 1923 to August 1927. The composition of each sample was determined as to species and at each collection the quantity of alga was noted. Miles Rough bog (see Fig. 1) is at the upper end of a glacial overflow channel in the Millstone Grit. It is about 25 m. in length and the same in breadth and lies at an altitude of some 220 m. At the upper western end is a steep slope, and from the base of the slope issues the water, chiefly by one spring, which flows over the bog and finds its exit at the lower eastern end. The bog is a sphagnum bog and scattered among the sphagnum are:

*Juncus bulbosus* L.

*Potentilla erecta* (L.) Hampe

*Viola palustris* L.

*Hydrocotyle vulgaris* L.

*Drosera rotundifolia* L.

*Carex flava* L.

Around the sphagnum but still in the bog the vegetation is dominated by *Juncus effusus* L., among which are *Cirsium palustre* (L.) Scop., and at the upper end *Nardus stricta* L. Clumps of *Holcus lanatus* L. occur. More occasional grasses are *Anthoxanthum odoratum* L., *Sicglingia decumbens* (L.) Bernh. and *Molinia cerulea* (L.) Moench. The vegetation surrounding the bog is acidic in character, including ling, bilberry, tormentil and gorse.

The samples were taken from numbered situations shown in Fig. 1, and of these 1, 5, 10 and Entry were shallow pools or shallow streams with muddy bottom, 7 and 8 were in the deep ditch at the bottom of the bog, 3 and 6 were on the borders of the sphagnum bog, 4 and 9 were in the middle of the sphagnum.

The water enters the bog at the base of a steep slope on the west side and flows over the bog into a ditch on the east, which discharges at the north-east corner. The chief entry is a single drain, but in wet times additional supplies enter. The water enters at an almost uniform temperature of about 8.0° C. all the year round. The minimum temperature recorded was 7.0° C. in December 1925 and the maximum 9.0° C. in July and in November 1926. As the water passes over the bog it is cooled in winter and warmed in summer. The highest water temperatures recorded were 24.5° C. in August 1926, 20.6° C. in July 1926, and 18.8° C. in July 1925, and the lowest were 1.2° C. in March 1924, 2.0° C. in February 1926, and 3.0° C. in March 1925.

The water is hard, containing considerable quantities of calcium sulphate. It is acid. pH values have been taken regularly by colorimetric methods and show that the entering water has a pH of 4.8–5.2 at different seasons of the year. On passing over the bog the water becomes slightly less acid and the lowest acidity is found in the centre of the bog among the sphagnum. A typical reading is that of 21 March 1927:

Entering water	pH = 4.9	Sphagnum pool	pH = 5.2
Bottom ditch	pH = 5.1 and 5.2	Most central sphagnum pool	pH = 5.4

## ALGAE PRESENT

## List of algae recorded

Chlamydomonas sp.	Tabellaria flocculosa Kütz.
Palmodictyon sp.	T. fenestrata Kütz.
Sphaerocystis Schroeteri Chod.	Eunotia praerupta var. Ehrenb.
Hormidium subtile Heer.	E. arcus Ehr. v. uncinata V. Heurck
Microspora floccosa (Vauch.) Thur.	E. pectinalis Kütz. var.
M. tumidula Hazen	Navicula major Kütz.
M. stagnorum (Kütz.) Lagerh.	N. viridis Ehrenb.
M. pachyderma (Wille) Lagerh.	N. viridis var.
? M. quadrata Hazen	N. legumen Ehrenb.
Stigeoclonium tenue Kütz.	N. bicapitata Lagerst.
Oedogonium rufescens Wittr.	? N. brevicostata Cleve
Oedogonium sp.	Stauroneis spicula
	Surirella linearis W.Sm.
Spirogyra sp.	S. linearis var. constricta Grun.
Zygogonium ericetorum Kütz.	S. biseriata Bréb.
Mougeotia viridis (Kütz.) Wittr.	S. ovalis Br. v. ovata Kütz.
M. parvula Hass.	
Mougeotia sp. 'with violet granules'	Merismopedia glauca (Ehr.) Naeg.
Mougeotia sp.	Oscillatoria tenuis Agardh.
Cylindrocystis Brebissonii Menegh.	? Chroococcus minutus (Kütz.) Naeg.
Penium Navicula Bréb.	Stipitococcus urceolatus W. & G. S. West
Closterium striolatum Ehrenb.	Dinobryon sertularia Ehrenb.
C. rostratum Ehrenb.	Synura uvella Ehrenb.
C. parvulum Naeg.	Chrysopyxis globosa Rich
C. subulatum (Kütz.) Bréb.	Cryptomonas sp.
Closterium sp.	? Gymnodinium sp.
Tetmemorus laevis (Kütz.) Ralfs	Euglena intermedia (Klebs) Schmitz
Euastrum binale (Turp.) Ralfs	Euglena sp.
Micrasterias denticulata Bréb.	Trachelomonas volvocina Ehrenb.
Cosmarium subtumidum Nordst.	
C. quadratum Ralfs var.	
Staurastrum punctulatum Bréb.	

Above is a list of all the algae known to be found in the bog. It shows the value of continuous examinations spread over a period of years, for this method has revealed in this small bog the presence of *Oedogonium rufescens* Wittr., only once before gathered in Yorkshire, *Sphaerocystis Schroeteri* Chod. new to the county, and *Chrysopyxis globosa* Rich, which is the first record in point of time of any species of *Chrysopyxis* in Great Britain, though its correct identification was not made until 1933 when Rich (1933) established this species from Leicestershire material. It was then found that the *Chrysopyxis* from this bog was identical with the species newly established by Rich.

In bulk the principal algae present were two species of *Mougeotia*, three species of *Microspora* and *Zygogonium ericetorum*. *Spirogyra* was almost absent. Of more than three hundred separate gatherings *Spirogyra* was only seen in three and then in only small amount. Common desmids were *Cylindrocystis Brebissonii* Menegh., *Closterium striolatum*, *C. parvulum*, *C. rostratum*, *Tetmemorus laevis*, *Cosmarium subtumidum*, and *Staurastrum punctulatum*.

The diatoms never bulked large, nor did the Myxophyceae. Of the Eugleninae, *Euglena intermedia* and another species were fairly common. Where it was certain from vegetative characters that a species existed, but no definite identification was possible, it has been entered under the genus. This is the case with an *Oedogonium*, a *Mougeotia*, a *Closterium*

and a *Euglena*. The *Oedogonium* was one of much larger dimensions than *O. rufescens*, but as it never showed any signs of sexuality it could not be identified. The most important of these non-determinable species was a *Mougeotia* (or *Debarya*). At times this formed a considerable bulk of alga. It was distinguished from *Mougeotia viridis* and *M. parvula*, by the constantly larger cell size and particularly by the presence in the cells of numerous granules. These granules were at times colourless, at other times coloured violet. The colouring when present was of varying intensity. At times there

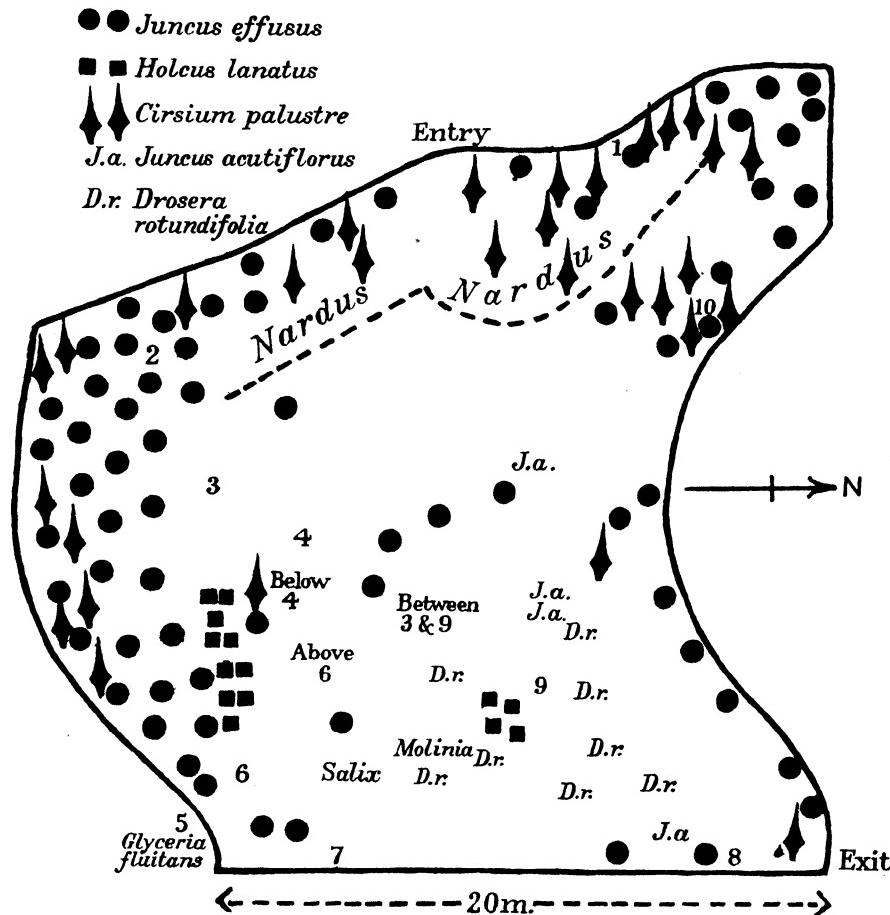


Fig. 1. Sketch-plan of bog.

was so much of this alga with the cells coloured fully violet that it formed conspicuous dark masses. It was chiefly present in the deepest water, that of the bottom ditch. In the tables it is named the '*Mougeotia* with violet granules', but it was possibly a *Debarya*. As it did not conjugate, it was impossible to identify it, yet it was important ecologically and was one of the species which gradually decreased in amount as the bog became more choked. It is almost certain, judging from dimensions and cell characters, that there was another species of *Mougeotia* which never conjugated, and the existence of these undetermined species, as well as the facts about *M. parvula* recorded below, show that species of *Mougeotia* exist for years without conjugation.

## SEXUAL REPRODUCTION

Sexual reproduction occurred in a few species only. These were *Mougeotia viridis*, *M. parvula*, *Oedogonium rufescens*, *Cylindrocystis Brebissonii*, *Closterium rostratum* and *C. parvulum*. It is noticeable that, in those species of this list which have decided preferences of habitat, conjugation only occurs in that habitat which is shown by records of abundant occurrence to be the favourite habitat of the species. This is shown clearly by *Mougeotia viridis* which never conjugated among sphagnum and by *Cylindrocystis Brebissonii* which never conjugated except among sphagnum. If the records are compared with those of other observers it appears that the tendency to resort to sexual reproduction is a specific character. The species *Mougeotia viridis* is very frequently found in conjugation, as is also *Cylindrocystis Brebissonii*. This is indicated by the frequency with which conjugation has been reported in the literature in these species. *Zygogonium ericetorum*, on the other hand, is very seldom found in conjugation. West (1916) wrote of it as a most obstinate alga refusing to conjugate through all kinds of external changes. The other species found in conjugation in the bog, viz. *Mougeotia parvula*, *Closterium rostratum* and *C. parvula*, are also frequently recorded and illustrated in conjugation. This point of view is opposed to one frequently taken about algae that reproductive processes are almost entirely dependent on external conditions and can therefore be experimentally varied. It does not appear to me that algae are more susceptible in this respect to external changes than are flowering plants, and it is probable that they are affected by very similar environmental conditions, the chief of which is sunlight. Just as a hot dry summer tends toward increased flowering, so do algae more frequently resort to sexual reproduction with greater exposure to sunshine.

## ALGAL GROWTH AND ENVIRONMENT

Table 1 shows the relation between the total amount of alga in the bog and the amount of water in the bog. The minimal amounts of alga, e.g. August 1923, August 1925, October 1926 and June 1927, are always related to previous dry conditions in the bog, and the maximal amounts with wet conditions, e.g. April 1923, January 1925, March 1926 and March 1927. The quantity of water in the bog being the main controlling factor in the growth of the algae, it is an interesting question whether there are other factors which occasionally modify its effect. It is possible that the reduced quantity of alga in March 1924 and the persisting low quantity in November 1926 were both due to the very low temperatures of those periods, but the equally frosty period in December 1925 had no diminishing effect, so that there is no certainty on this point. Secondary minima intervened in March 1924 and March 1925 between the maxima of December and April, and in 1924 this occurred without any diminution of water supply to account for it. On the other hand, no such secondary minimum occurred in March 1926. The amount of alga remained without diminution from December to April.

Whether maxima of December and April were regularly separated from each other by a secondary minimum or not, it is worth while to examine whether the composition of the algal bulk was the same at these two periods. Close examination of the records for the different years shows that all through the winter from November to April the bulk of the alga consisted of three species of *Microspora*, viz. *tumidula*, *stagnorum* and *floccosa*,

the '*Mougeotia* with granules', and *Zygogonium ericetorum*, with some *Mougeotia viridis* in some years. The April maximum still consisted chiefly of these, but had *M. viridis* regularly in good amount and showed in addition *M. parvula* and one or perhaps two unnamed species of *Mougeotia*. The increase of *M. viridis* and the occurrence of the additional species of *Mougeotia* was offset in April by some decrease of the typically winter species, so that the bulk of alga usually remained about the same.

Having recorded the relative abundance of total alga in the bog an attempt was made to make similar records of bulk for single species of alga. This could only be done for two of the most abundant species, as it depended on an estimate of the relative abundance of the particular species in each sample collected throughout the investigation. This estimate could not be made with any accuracy for scarce species. Reliable data were obtained for two species, the '*Mougeotia* with granules' and *Zygogonium ericetorum*. The noteworthy points shown by these data were that the *Mougeotia* was a 'summer' type

Table 1

	State of bog	Total alga		State of bog	Total alga
1923	Apr. Wet	A	1925	Sept. Mod. wet	C -
	May Mod. wet	B		Oct. Mod. wet (drier)	B
	June Mod. wet (drier)	B		Dec. Very wet	A -
	July Rather dry	C		Feb. Very wet	A -
	Aug. Dry	C -		Mar. Wet	A
	Oct. Mod. wet	B		Apr. Dry	B -
	Nov. Very wet	B +		May Mod. wet	B -
	Jan. Very wet	B +		June Wet	C +
	Mar. (Snow) very wet	C		July Dry	C
	Apr. Mod. wet	A -		Aug. Dry	C -
1924	May Wet	B -		Sept. Very dry	C -
	June Mod. wet	B		Oct. Wet	D
	Oct. Very wet	C		Nov. Very wet	D
	Nov. Very wet	B		Dec. Wet	A
	Dec. Very wet	A -		1927 Jan. Mod. wet	B
	Jan. Mod. wet	A -		Feb. Very wet	B
	Feb. Very wet	B +		Mar. Wet	A
	Mar. Rather dry	B		Apr. Mod. wet	A
	May Wet	A		May Mod. wet (drier)	B -
	June Rather dry	B		June Very dry	C -
1925	July Dry	C -		July Mod. wet	C
	Aug. Rather dry	D		Aug. Very wet	C +

A = abundant; B = good amount; C = scarce; D = almost absent.

usually having its maximum occurrence in June, that it was subject to sudden and violent fluctuations apparently depending on water supply, and that it diminished steadily in average amount throughout the period of investigation. The *Zygogonium*, on the other hand, usually had its maximum occurrence in December, was subject to less violent fluctuations, presumably because, living among the sphagnum, its water supply was much steadier, and increased steadily in average amount through the whole period. The steady increase of *Zygogonium* and decrease of the *Mougeotia* were due to the gradual choking of the bog drainage, a feature which will be discussed later. Further examination of the detailed records shows that the '*Mougeotia* with granules' was an alga of the ditch, stream and pools not on sphagnum. It appeared in very large quantity in the ditch in April and May 1923, December 1924 and May 1925, and at these times its dark colour made it conspicuous.

More detailed records for *Zygogonium ericetorum* show that it appeared in the ditch in June, September and October 1925 after a large mass of '*Mougeotia* with granules'

had disappeared, and the same sequence occurred again in its appearance in March 1927 in a mud-bottomed pool from which a fairly large amount of the '*Mougeotia* with granules' had recently disappeared. It is thus possible that this 'water' form of the *Zygomonium* (distinguished by its longer cells) depends to some extent on the presence of decaying organic matter. If so, it resembles the 'land' form of the same alga, which is widespread on bare wet peat where presumably considerable amounts of organic matter are available.

#### OCCURRENCES OF SEPARATE SPECIES

For each species tables have been made summarizing its occurrence in various parts of the bog. A column is given to each position from which collections were made. The positions on the sphagnum are on the right, the waters of the deeper ditch in the centre, and the shallow pools and runlets not on sphagnum, but with muddy bottom, are on the left. Each position is marked on the sketch-plan (Fig. 1). Positions 3 and 6, which were on the sphagnum but close to deeper water, are placed between the two sets. In the columns are placed all the observations of occurrence. Mere occurrence is denoted by D, in small quantity by C, in larger amount by B and A in order, and the letters may be modified by + or - : thus A+ means great abundance, A- in considerable amount. Reproduction of any kind is denoted by a star. In the few cases where zygotes only occurred zyg. is added to the letter. Table 2 gives data for *Mougeotia viridis*. It shows first of all that this is an alga of the ditches and pools not on sphagnum. Its occurrence on sphagnum is sporadic and always in small amount only. This alga conjugates frequently, regularly in spring, beginning in March or April and going on to June in some part or other of the bog. In any one position the sequence is usually conjugation one month, conjugation mixed with ripe zygotes the next, ripe zygotes only the next, and this cycle is usually followed by complete disappearance in the next month. A second period of conjugation occurred in late summer or autumn if the bog was not too dry. The onset of this varied from July to September in different years, and zygotes from this autumn conjugation were found in November (1924) and even as late as December (1925). The only months without either conjugation or zygotes were January and February. In these months the alga was never found in more than moderate quantity. It was very much reduced in amount by the dry late summer of 1926, the September collection only yielding one very small amount and the November collection none at all. It returned in small amount in three separate pools in December.

Table 3 gives data for *Microspora floccosa*. This was very strictly confined to the sphagnum, only appearing off it on very rare occasions. It showed more clearly than any other alga the effect of the drainage of the bog in May 1923. Whereas in April of that year it had been abundant in three sphagnum pools, it decreased steadily after the draining until April 1924, when it was apparently absent from the whole bog. Then it reappeared and increased steadily and regularly in amount up to the end of the period, the maximum amount of the whole 4½ years being found in July 1927. Fritsch & Rich (1913) wrote of the *Microsporas* as algae of low temperatures, but *M. floccosa* was found here at its maximum for 1927 in July and for 1926 in August. The temperature of the sphagnum water at the latter date varied from 19.2 to 24.5° C., and on the former from 11.5 to 15.7° C. These temperatures are not absolutely high perhaps, but only relatively to the average in this northern habitat, and thus it is possible to consider that the record

falls into line with the usual statements. It would, however, be more accurate not to lump all the species of *Microspora* together with respect to temperature. As the records of *M. tumidula* Hazen show, this alga had its maxima at quite a different time of the year as follows: 1924 January, 1925 December, 1926 March, 1927 March. These are all in the coldest period of the year. Its minima are in August in 1925, 1926 and 1927 and

Table 2. Occurrence of *Mougeotia viridis*

Date	Shallow pools and stream				Ditch				Sphagnum				
	Near				Between				Above	4 and	9	Between	
	1	1	5	10	7	7 and 8	8	3	6	6	below	9	3 and 9
20. iv. 23	A*	.	A*	A*	.	.	.	B - *	B - *	.	.	.	.
v. 23	A*	.	A	.	B*	.	.	C*	.	.	.	.	.
vi. 23	.	.	C	.	.	.	B*	C	B*	.	.	.	.
vii. 23	.	.	.	.	Zyg.	.	.	.	.	.	.	.	.
viii. 23	.	.	.	.	.	.	.	.	.	.	.	.	.
x. 23	.	.	C	C	B -	.	.	.	C	.	C	.	.
xi. 23	C	.	.	C +	A	.	B	C	.	B	.	C	.
i. 24	.	.	C	.	C	.	B	.	C	.	C	.	.
iii. 24	.	.	.	.	A	.	.	.	C	.	.	.	.
iv. 24	B + *	.	.	C	A +	.	.	.	C	.	.	.	.
iv. 24	B - *	.	.	B -	A - *	.	D	.	C	.	.	.	.
v. 24	C	.	C	A *	A - *	.	.	C *	.	.	.	.	.
vi. 24	C	.	.	.	C	.	.	.	.	.	.	.	.
x. 24	.	.	C	C	.	.	.	.	.	.	.	.	.
xi. 24	.	.	.	C	A zyg.	.	D	.	.	.	.	.	.
xii. 24	.	.	.	C +	.	.	.	.	.	.	.	.	.
i. 25	C	.	.	.	.	.	.	.	.	.	.	D	.
iii. 25	C	.	.	.	.	.	.	.	.	.	.	.	.
iii. 25	C *	.	.	C	.	.	C	.	.	.	.	.	.
v. 25	C *	.	.	C *	B *	.	B + *	.	.	.	.	.	.
vi. 25	B *	.	.	B *	B zyg.	B + * zyg.	.	.	.	.	.	.	.
vii. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
viii. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
ix. 25	.	.	.	.	.	B *	.	.	.	.	.	.	.
x. 25	.	C +	.	C + *	A -	B + zyg.	B	.	.	C	.	C	.
xii. 25	.	C +	.	C	C	.	B	.	C	C	.	C	.
ii. 26	B	.	C	C	.	.	.	.	C	C	.	C	.
iii. 26	B +	.	.	.	.	.	.	.	C	C	.	C	.
iii. 26	B *	.	C	.	.	B -	.	B +	.	C	.	C	.
iv. 26	B - zyg.	.	C zyg.	B	.	B zyg.	B	B + *	C	.	.	C	.
v. 26	C zyg.	.	C *	.	.	.	.	.	.	.	.	.	.
vi. 26	C	.	.	.	.	.	.	D	.	.	.	.	.
vii. 26	C *	.	.	.	.	.	.	.	.	.	.	.	.
viii. 26	C zyg.	.	.	.	.	.	.	.	.	.	.	.	.
ix. 26	.	.	.	D	.	.	.	.	.	.	.	.	.
xi. 26	.	.	.	.	.	.	.	.	.	.	.	.	.
xii. 26	.	.	C	C	C	C	.	.	C	.	D	C	.
i. 27	C	.	.	C	B -	C	.	.	.	C	.	C	.
ii. 27	.	.	.	B -	B	B	B *	.	.	.	.	.	.
iii. 27	B *	.	B -	B	B	B *	.	.	.	.	.	.	.
iv. 27	B *	.	A - *	A - *	A *	A *	.	.	B	.	.	.	.
v. 27	B *	.	B *	C *	C *	B *	.	C	.	C	.	.	.
vi. 27	C zyg.	.	.	C zyg.	C zyg.	C zyg.	C *	.	C	.	.	.	.
vii. 27	.	.	D	C	.	.	.	.	.	.	.	.	.
viii. 27	.	A *	.	.	.	.	.	.	.	.	.	.	.

• Symbols as in Table 1.

in October in 1924, no August observations having been made in that year. The records of *M. stagnorum* (Kütz.) Lagerh. are very similar in this respect to those of *M. tumidula*. Both these are algae of the deeper water of the ditch, and it was not therefore from entire lack of water that they were absent in August, since this ditch always retained some water. It seems probable therefore that *M. tumidula* and *M. stagnorum* are typical cold-water algae, while *M. floccosa* is not so, but is capable of flourishing at higher temperatures.

*The algae of Miles Rough bog, Bradford*

The records of *M. tumidula* show that it is an alga primarily of the deeper water, there being only one record of any significant quantity on the sphagnum. Furthermore, all the records of asexual reproduction were in the deeper water of the ditch or very near it, so that it is confirmed, as in *Mougeotia viridis*, that reproduction only occurs in the

Table 3. Occurrence of Microspora floccosa

Date	Shallow pools and stream				Ditch			Sphagnum			
	1	2	5	10	7	Between 7 and 8	8	Above 6	3, 4 and below	9	Between 3 and 9
20. iv. 23	.	.	.	.	.	.	.	A	A	B	.
v. 23		Bog drained			.	.	.		A	C	.
vi. 23	.	.	.	.	.	.	.	B	B	.	.
vii. 23	.	.	.	.	.	.	.	B +	A -	.	.
viii. 23	.	.	.	.	.	.	.	.	.	.	.
x. 23	.	.	.	.	.	.	.	+	A -	.	.
xi. 23	.	.	.	.	.	.	.	.	C	.	.
i. 24	.	.	.	.	.	.	.	.	.	C	.
iii. 24	.	.	.	.	.	.	.	.	.	C	.
iv. 24	.	.	.	.	.	.	.	.	.	A	.
iv. 24	.	.	.	.	.	.	.	.	.	A	.
v. 24	.	.	.	.	.	.	.	.	.	A	.
vi. 24	.	.	.	.	.	.	.	C	C	.	.
x. 24	.	.	.	.	.	.	.	C +	C	A	.
xi. 24	.	.	.	.	.	.	.	C +	C	A	.
xii. 24	.	.	.	.	.	.	.	C	C	A	.
i. 25	.	.	.	.	.	.	.	C	C	A	.
iii. 25	.	.	.	.	.	.	.	C	C	A	.
iii. 25	.	.	.	.	.	.	.	C	C	C	.
v. 25	.	.	.	.	.	.	.	.	B +	.	.
vi. 25	.	.	.	.	.	.	.	C	B	.	.
vi. 25	.	.	.	.	.	.	.	C	B	.	.
vii. 25	.	.	.	.	.	.	.	.	B	.	.
viii. 25	.	.	.	.	.	.	.	C +	B +	.	.
ix. 25	.	.	.	.	.	.	.	B -	B +	.	.
x. 25	.	.	.	.	.	.	.	B -	B +	.	.
xii. 25	.	.	.	.	.	.	.	B	A	.	.
ii. 26	.	.	.	.	.	.	.	A	A -	.	.
iii. 26	.	.	.	.	.	.	.	.	A	.	.
iii. 26	.	.	.	.	.	.	.	.	A	.	.
iv. 26	.	.	.	.	.	.	.	.	A	.	.
v. 26	.	.	.	.	.	.	.	C	A	A -	.
vi. 26	.	.	.	.	.	.	.	C	B	A -	.
vii. 26	.	.	.	.	.	.	.	.	A -	A -	C
viii. 26	C	.	.	.	.	.	.	B -	B	B +	C
ix. 26	.	.	.	.	.	.	.	D	B -	B	D
x. 26	.	.	.	.	.	.	.	.	.	.	.
xi. 26	.	.	.	.	.	.	.	C +	.	B -	C
xii. 26	.	.	.	.	.	.	.	A	A	A -	C
i. 27	.	.	.	.	.	.	.	A	A	A	C
ii. 27	.	.	.	.	.	.	.	A	A -	A	C
iii. 27	C	.	.	.	.	.	.	B	A -	A	C
iv. 27	.	.	.	.	.	.	.	.	A -	A	.
v. 27	.	.	.	.	.	.	C	C	A	A	.
vi. 27	C	.	.	.	.	.	.	C	A -	A -	C
vii. 27	C	.	.	.	.	.	.	B +	B +	A -	B +
viii. 27	C	.	.	.	.	.	.	.	A	A	C

Symbols as in Table 1.

habitat where growth flourishes. Zoospores were observed in February, March, May and June, and were always followed by rapid diminution of the quantity of the alga in that place.

*Microspora stagnorum* (Kütz.) Lagerh. had very similar records to those of *M. tumidula*, except that no reproduction was certainly observed.

*Oedogonium rufescens* Wittr. is shown in Table 4. It was never abundant in quantity, but was very generally spread over the bog in all the different types of habitat. It was perhaps more persistent among the sphagnum. Reproductive organs, usually oogonia, were observed at intervals throughout the year (March, April, May, June, July and October), and after the dry late autumn of 1926, when plenty of rain came again, they

Table 4. Occurrence of *Oedogonium rufescens*

Date	Shallow pools and stream				Ditch				Sphagnum				
	1	2	5	10	7	Between 7 and 8	8	3	6	Above 6	4 and below	9	Between 3 and 9
20. iv. 23	.	.	.	.	.	.	.	.	.	.	.	.	.
v. 23	.	.	.	.	.	.	.	+	*	.	.	.	.
vi. 23	.	.	.	.	.	.	.	.	.	.	.	.	.
vii. 23	.	.	.	.	.	.	+	*	.	.	.	.	.
viii. 23	.	.	.	.	.	.	+	.	.	.	.	.	.
x. 23	.	.	.	.	.	.	.	.	.	.	.	*	.
xi. 23	.	.	.	.	.	.	.	.	.	.	.	.	.
i. 24	.	.	.	+	.	.	.	.	.	.	+	.	.
iii. 24	.	.	.	.	.	.	++	.	.	.	.	.	.
iv. 24	.	.	.	.	.	.	.	.	.	.	++	.	.
iv. 24	.	.	.	.	+	+	.	.	.	.	.	+	.
v. 24	.	.	.	.	.	.	.	.	.	.	.	.	.
vi. 24	.	.	.	.	.	.	.	.	.	.	.	*	.
x. 24	.	.	.	+	.	.	.	.	.	.	.	.	.
xii. 24	.	.	.	.	.	+	.	.	.	.	.	.	.
xii. 24	.	.	.	.	.	.	.	.	.	.	.	+	.
i. 25	.	.	.	.	.	.	.	.	.	.	.	+	.
iii. 25	.	.	.	.	.	.	.	.	.	.	.	+	.
iii. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
v. 25	.	.	.	.	.	.	.	.	.	.	.	+	.
vi. 25	.	.	.	.	.	.	.	.	.	.	.	+	.
vii. 25	.	.	.	.	.	.	.	.	.	.	.	.	+
viii. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
ix. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
x. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
xii. 25	.	.	.	.	.	.	.	.	.	.	.	.	.
ii. 26	.	.	.	+	.	.	.	.	.	.	.	+	.
iii. 26	.	.	.	.	.	.	.	.	.	.	.	.	.
iii. 26	.	.	.	.	.	.	.	.	.	.	.	*	.
iv. 26	.	.	.	.	.	.	.	.	.	.	*	.	.
v. 26	+	.	.	.	.	.	.	.	.	.	.	.	.
vi. 26	.	.	.	*	.	.	.	.	.	.	.	.	.
vii. 26	.	.	.	.	.	.	.	.	.	.	.	.	.
viii. 26	.	.	.	.	.	.	.	.	.	.	+	+	.
ix. 26	+	.	.	.	.	.	.	.	.	.	+	.	.
xi. 26	.	.	.	.	.	.	.	.	.	.	.	.	.
xii. 26	.	.	.	.	.	.	.	.	.	.	+	?	.
i. 27	.	.	.	+	.	.	.	.	.	.	*	.	.
ii. 27	.	.	.	.	.	.	.	.	.	.	.	.	.
iii. 27	.	.	.	.	.	.	.	.	.	.	.	+	.
iv. 27	.	.	.	.	.	.	.	.	.	.	.	.	.
v. 27	.	.	.	+	.	+	.	+	+	*	.	.	.
vi. 27	.	.	.	*	.	+	.	+	+	.	.	+	.
vii. 27	.	.	.	.	+	+	.	+	+	.	.	+	.
viii. 27	.	.	.	.	.	.	.	.	.	.	.	.	.

Symbols as in Table 1.

were found in December and January, so that the sexual reproduction of this alga is mainly a summer one, but it may in special circumstances reproduce again in late autumn or winter. The best development with abundant antheridia present was in June 1926. Reproduction was found in every type of habitat.

The foregoing were the main filamentous algae found. The desmids next claim our attention.

*Cylindrocystis Brebissonii* Menegh. was a sphagnum desmid primarily, though frequently occurring in the other habitats also. Conjugation was only observed on the sphagnum. It showed a decided tendency throughout the period to spread with the sphagnum when the latter extended its area owing to poor drainage. Thus it was far the most abundant in 1927, the last year of the observations. In this year it was most widespread and abundant in May. Its conjugation was observed in 1924, 1926 and 1927 and occurred in each of these years in both May and June. No conjugation was observed in 1925. Since the species conjugated so regularly in other years it might be thought that some special circumstance could be found to account for the absence of conjugation in 1925. But the records show nothing to which this could be traced. The previous year was the wettest summer of the period, but 1925 itself was by a little the driest. It is to be inferred from the restriction of conjugation to May and June that sunshine favoured it, but it seems unlikely that the duller weather of the summer of 1924 could affect the conjugation a year later.

*Cladostelium rostratum* Ehren. was a desmid of the deeper water chiefly, spreading slightly to the sphagnum. It showed conjugation in each year of the period except 1927, which was an incomplete year. Conjugating cells were found in April and June 1923, July 1926 and October 1925, while zygotes were found in November 1924. It was not a frequent desmid and it disappeared for long periods (up to 12 months) after conjugation.

*C. striolatum* Ehren. was found primarily in the deeper water and in the pools on mud, there being only one record of its having been found in quantity on sphagnum. It was much more frequent and sustained in its appearance than *C. rostratum*. It was found in considerable quantity in all months except February, August and September. It seems clear, since the fate of the zygotes is to fall through the water to the substratum below, that a successfully conjugating alga will disappear from the upper water after zygote formation and so will be less regular and continuous in its appearances in the water than a non-conjugating one. This is illustrated by the records of these two species of *Cladostelium*.

*C. parvulum* Naeg., unlike the two previous species, was distributed generally over the bog in all the different habitats. It was present in good quantity in January, March, April, June, October and November. It was found in conjugation once only, viz. April 1926. This occurrence was in a shallow stream.

*C. subulatum* (Kütz.) Bréb. was found infrequently in all positions which were not on sphagnum. It was gathered in quantity only in January and April.

*Tetmemorus laevis* (Kütz.) Ralfs was a typical sphagnum desmid, occurring regularly and in increasing quantity on the sphagnum, straying occasionally into deeper water and grassy pools, but never establishing itself there. Its maxima for quantity occurred in January, June and July, and its minima March, August and September.

*Euastrum binale* (Turp.) Ralfs was found almost entirely on the bog moss, but in much smaller quantity and less regularly than was *Tetmemorus laevis*. Nevertheless, the steady increase which followed the choking of the bog is seen clearly in its record and is shown in both quantity and range.

Two other desmids, *Cosmarium subumidum* Nordst. and *Staurastrum punctulatum* Bréb., were found in considerable quantity frequently and in all the habitats.

Of the sixteen species of Bacillariales found, it may be said in general that there was no evidence of the winter maximum of these organisms which is frequently found,

especially in plankton investigations. They were found in comparatively large quantity as follows: *Surirella* spp. in April and June, *Navicula* spp. in January, June, October and November, *Tabellaria flocculosa* in January, February, May, October and December. They did not form an important part in bulk of the algae collected. Their position here is quite different from their position in the plankton of either salt or fresh water. The different species showed individual preferences of habitat, just as the other algae did. For instance, the chief species of *Navicula* were found mainly among sphagnum, to some extent in the shallow pools, but not in the deeper water of the ditch. *Tabellaria flocculosa* Kütz. was chiefly found in the deeper water though to some extent also on sphagnum, while *Surirella linearis* W.Sm. and *S. biseriata* Bréb. were restricted to the shallow pools and not found either in the deeper water or on sphagnum. It was among the diatoms in fact and chiefly in the cases of *Surirella* spp. and *Tabellaria flocculosa* that evidence was found that the non-sphagnum habitats ought not to be considered as one, but showed a difference between those having deeper water and those having shallow water.

#### MYXOPHYCEAE

Two of this group occurred fairly frequently and both were found in the bog-moss pools, *Merismopedia glauca* (Ehr.) Naeg. being strictly confined to these, while *Oscillatoria tenuis* Agardh. also occurred occasionally and in small quantity in the shallow stream and deeper ditch.

Observations on the following three algae gave the results stated:

(1) *Sphaerocystis Schroeteri* Chod. of the Volvocales was a generally distributed alga, but occurring somewhat more frequently on the sphagnum. It occurred at all times of the year, the highest quantity records being in October and November.

(2) *Euglena intermedia* (Klebs) Schmitz was found in all the habitats and in every month of the year.

(3) *Synura uvella* Ehrenb. (Chrysophyceae) was fairly evenly distributed over all the habitats and in every month except July and December. This is stated (West & Fritsch, 1927) to follow on recent rains, and the idea is to some extent supported by my records, for example, the record of September 1925 was after three very wet days, while there was no occurrence in September 1926 when the weather was dry.

Thus there were in the bog two main algal associations:

I. The free-water association from the shallow pools on mud, the shallow stream and the deeper ditch. The dominant algae of this association were the '*Mougeotia* with granules', *M. viridis*, *Microspora tumidula* and *M. stagnorum*. The subordinate members were:

<i>Hormidium subtile</i>	f.	<i>Closterium subulatum</i>	r.
<i>Mougeotia parvula</i>	f.	<i>Micrasterias denticulata</i>	r.
<i>Oedogonium rufescens</i>	o.	<i>Tabellaria flocculosa</i>	f.-a.
<i>Closterium striolatum</i>	a.	<i>Surirella</i> spp.	o.
<i>C. parvulum</i>	f.	<i>Sphaerocystis Schroeteri</i>	f.
<i>Cosmarium subtumidum</i>	f.	<i>Euglena intermedia</i>	o.
<i>Staurastrum punctulatum</i>	f.	<i>Synura uvella</i>	o.
<i>Closterium rostratum</i>	o.	<i>Palmodictyon varium</i>	v.r.
<i>Cylindrocystis Brebissonii</i>	o.		

II. The association of the sphagnum pools. The dominant algae of this association were *Zygomonium ericetorum* and *Microspora floccosa*. The subordinate members were:

<i>Oedogonium rufescens</i>	f.	<i>Navicula</i> spp.	f.-a.
<i>Hormidium subtile</i>	o.	<i>Tabellaria flocculosa</i>	o.
<i>Cylindrocystis Bréb.</i>	f.-a.	<i>Merismopedia glauca</i>	f.
<i>Tetmemorus laevis</i>	f.-a.	<i>Oscillatoria tenuis</i>	f.
<i>Cosmarium subtumidum</i>	f.-a.	<i>Sphaerocystis Schroeteri</i>	f.
<i>Closterium parvulum</i>	f.	<i>Euglena intermedia</i>	o.
<i>Staurastrum punctulatum</i>	f.	<i>Synura uvella</i>	r.
<i>Euastrum binale</i>	r.		

#### SECULAR CHANGES

The tables show not merely periodicity, but changes spreading over the whole period. Certain algae, e.g. *Zygomonium ericetorum*, *Microspora floccosa*, increased in quantity and extended their range steadily during the whole period. Their dependent algae, *Cylindrocystis Brebissonii* and *Tetmemorus laevis*, showed the same change. Other algae, particularly the '*Mougeotia* with granules', became gradually more restricted in range and appeared in smaller quantity. Thus the sphagnum algae steadily gained during the five-year period, the clear-water algae lost ground. The cause of this steady gain of one association of algae over another lay in the general drainage of the bog. It was noticed that in May 1923 the bottom ditch was cleared and made wider. This observation was made, of course, long before the gradual changes in the algae were apparent, since these did not become clear until records of distribution and quantity were made at the very end of the five-year investigation. The opening of the bottom ditch made a clearer channel there with more free water and also lowered the level of the water among the sphagnum. There followed the period of greatest abundance and extent of the members of the free-water association. Then came a long slow blocking up of this channel which restricted the open water and raised the level of the water among the sphagnum. The sphagnum itself invaded the channels and the consequent gradual spread of the sphagnum algae is clearly seen in the tables. For example, the table for *Microspora floccosa* shows a decrease, almost to a disappearance, of this alga after the drainage of the bog in May 1923, followed by a steady increase and spread up to the end of the investigation. Not only is this secular change found in the larger algae present at times in considerable bulk, but it is shown just as clearly by some of the smaller ones. Thus *Closterium rostratum* shows an increase following the drainage of the bog, followed by a decrease for the rest of the period, while on the other hand *Tetmemorus laevis* shows just as clearly a steady increase and spread through all the later years. It is specially significant of the fundamental nature of this gradual change that it should be obvious even in the records of an infrequent desmid, *Euastrum binale*, of a subordinate and occasional blue-green alga *Oscillatoria tenuis*, and of the diatoms as is seen from the records of the chief species of *Navicula* which, occurring principally on the sphagnum, showed the same gradual increase as was exhibited by the other members of the sphagnum association. This secular change in the bog was indicated also by the records of one of the flowering plants, *Drosera rotundifolia* L., which is well known to depend upon sphagnum for a suitable habitat. The *Drosera* plants were counted in the last three years of the investigation and the records were: 1925, 92 plants; 1926, 116 plants; 1927, 132 plants.

#### WATER CONDITIONS

Two problems present themselves in a closer analysis of the algal associations and their environment:

(1) What are the governing conditions of the environment which maintain the algal associations in general?

(2) What differentiating factors cause the two different algal associations to appear?

Analyses of the water were obtained in order to shed light on these questions. The view has been expressed by Griffiths (1923) that, since algae are subordinate to macrophytic vegetation, their occurrence and distribution will not depend directly upon the initial water supply of a bog or other area of water, although this seems to be their environment, but will depend upon this water supply as altered by the growth of macrophyta. On this view the soluble products liberated by the macrophyta in their growth or decay should be the chief cause of differences in algal growth. The nearest approach to this factor that can be obtained is the soluble organic content of the water, for which data are given below.

*Organic matter of Miles Rough bog in parts per 100,000*

	9 March	20 April	1 June
Inlet	3.5	6.0	—
Middle among sphagnum	5.0	—	5.5
Outlet	6.0	7.5	6.0

It appears from these figures that in the bog there was an increase in organic matter as the water passed over the bog. The middle position, among sphagnum, was intermediate between the two and lower than that of the outlet. In consequence this factor does nothing to cause the differences between the two chief algal associations, one of which occupies both the waters of the inlet and of the outlet, while the other flourishes in the middle position.

Detailed analyses of the water which enters the bog and the water which leaves it were made in 1928 and Table 5 shows the results.

Table 5. *Water analyses\*—constituents in parts per 100,000*

Source	28 April		7 June		Heather Glen, 13 May	
	Inlet	Outlet	Middle	Outlet	Inlet	Outlet
Temperature at collection, °C.	7	4	16	11.5	—	—
Total saline matter	21	23.5	19.0	19.0	21.0	14.5
Organic matter	6.0	7.5	5.5	6.0	4.5	3.5
Lime (CaO)	3.4	3.4	3.0	3.3	3.2	2.1
Magnesia (MgO)	1.01	1.37	1.44	1.3	0.79	0.83
Potash and soda ( $K_2O + Na_2O$ )	1.55	1.32	1.59	1.06	2.60	1.38
Nitrates as $N_2O_5$	1.66	0.447	0.08	0.12	2.80	0.09
Phosphates as $P_2O_5$	0.061	0.061	0.03	0.03	Tr.	Tr.
Iron (Fe)	0.015	0.015	0.15	0.15	0.02	0.025
Oxygen absorbed from permanganate at 27° C. in 2 hr.	0.036	0.068	0.059	0.11	0.097	0.13
Free carbondioxide ( $CO_2$ )	2.8	1.4	0.7	3.2	0.70	0.55

Apart from the increase in easily oxidizable organic matter shown by the oxygen absorbed from permanganate, the figures of chief significance here are those of the nitrate which sink from approx. 1.7 to 0.45 in April and to 0.10 in June. The same result is indicated by analyses (in 1929) of the water of another similar bog about 3 miles away (Heather Glen, Bingley).

Minor considerations apart, these figures show the same general result as those for Miles Rough bog, i.e. that the significant figures are those for the nitrate. This fact of

\* The cost of these and subsequent analyses has been defrayed by grants from the British Association, which are gratefully acknowledged.

the importance of nitrate content may therefore be considered as established for this type of bog, namely, the bog on the Millstone Grit, surrounded or partly surrounded by cultivated land and receiving drainage from such land. It has already been stated that the total amount of alga is correlated with the amount of water in the bog. It seems clear now that this water is needed not only in itself, but as bearing considerable quantities of the essential foodstuff nitrogen. The low amounts of alga usually found in June and July may be due primarily to lack of nitrate, which, as analyses show, is very small in amount at this period in the middle and at the exit of the bog. The sphagnum especially is not by any means devoid of water at this season but this water is so low in nitrate content that it apparently proves a limiting factor to the growth of algae. Further analyses were undertaken to get the distribution of this critical factor nitrate at different seasons of the year. The nitrate content at or near the water inlet and at or near the outlet is given in the following summary. In this, the results are given in the order of the months irrespective of the year in which they were obtained.

It appears from these facts of nitrate content that water pretty rich in nitrate enters the bog at all seasons when water is flowing into it at all. In winter only a little of

Place	...	Miles Rough bog				Heather Glen		Miles Rough			
		1931	1928	1930	1929	1930	1930	Inlet	Outlet	Inlet	Outlet
Year	...	2 March	20 April	23 April	13 May	6 June	13 November	Date	...		
N <sub>2</sub> O <sub>5</sub> in parts per 100,000		Inlet 1.95	Outlet 1.64	Inlet 1.66	Outlet 0.45	Inlet 1.97	Outlet 1.17	Inlet 2.80	Outlet 0.09	Inlet 1.54	Outlet 0.09
Difference between inlet and outlet		0.31		1.21		0.80		2.71		1.45	
											0.17

this nitrate is used up so that algae in all parts have a rich supply of nitrate. This is an important consideration when it is known from Table 1 that algae are often abundant in the depth of winter. Thus in December 1924 and January 1925, in the period from November 1925 to March 1926 and in December 1926 the total amount of alga in the bog was at its maximum. In the summer months, on the other hand, the nitrate becomes very low in quantity, particularly in the outlet. From the analyses it is seen that the nitrate becomes low in May and June even when nitrate-rich water is entering. If water ceases to enter, as occurred on 1 June 1928, the nitrate reaches a very low figure. The figures for the middle of the bog among sphagnum and for the outlet in the ditch on that date were 0.08 and 0.12 parts per 100,000 respectively. It is not surprising, therefore, that in June the quantity of alga is each year on the down grade and that, since the effect will be progressive, the lowest ebb should occur in July and August. To what we are to attribute this rapid use of nitrate is from our point of view of secondary importance. It is obvious that the macrophytic vegetation will use more of it in the summer, which is of course the time of maximum growth. It is also in the summer that we have in the bog conditions favouring denitrification. According to Russell (1917) these are (1) presence of nitrate, (2) presence of easily decomposable organic matter, (3) lack of oxygen. All these conditions are fulfilled in the bog and at summer temperatures no doubt appreciable denitrification must occur. Whatever may be the cause the primary result is a very low nitrate content in summer with its inevitable effect upon algal growth.

Another fact of analysis, namely the slight but steady decrease of acidity as the water passes over the bog, may receive its explanation also from this nitrate absorption. Prof.

Rideal has pointed out to me that if nitrates are consumed as nitric acid through a semi-permeable plant membrane the ions of calcium and magnesium will be driven over to combine with the  $H_2CO_3$ , and the analyses indicate that there is by no means sufficient  $H_2CO_3$  to maintain all the  $Ca^+$  and  $Mg^+$  as bicarbonate. Thus these ions would go over to the fully neutralized condition and render the water less acid.

So far no reason for the very clear differences between the algal association on the sphagnum and that in the pools and ditches has been given. The sphagnum is obviously a very different environment from either the water of the shallow pools or the deeper ditches. One way in which the sphagnum forms a very special environment is in slowing down the rate of the water passing through it. The water in the shallow pools, in the shallow runlet where position no. 10 was situated and in the deeper ditch often runs rapidly, but at all times the rate through the sphagnum is much slower. This no doubt has important effects on the algae because it tends to curtail the supply of various essentials, of nitrate in particular, but also of carbon dioxide and oxygen. In the case of food factors which are limiting, as nitrate has been shown to be, this stagnancy of the water in the sphagnum might be expected to lower the nitrate figures further than in those parts where a more vigorous current is bringing in fresh supplies at a greater rate. More detailed analyses for nitrate in different positions in the bog were taken as follows:

*Data as parts per 100,000\**

	Inlet and shallow pools	Sphagnum	Deeper ditch and outlet
Average $N_2O_5$	1.78	1.21	0.74
No. of samples	12	11	7

This is according to expectation, for all the shallow pools were near the inlet at the upper end of the bog, the sphagnum was in the middle and the deeper ditch at the bottom, so on the average we are here noting the gradual absorption of nitrate as it passes over the bog. But on one or two occasions the sphagnum water showed a lower nitrate content than any other part. This occurred on 1 June 1928 when among sphagnum the figure was 0.08 parts per 100,000, while near the exit 0.12 parts per 100,000 were found, and also on 13 November 1930 when one sphagnum pool showed only 0.92 while the inlet had 1.79 and the outlet 1.62. It cannot be said that this lower nitrate content could be the sole or even the main cause of the very different algal association on the sphagnum, because it is according to the analyses too occasional an occurrence. Nevertheless the sphagnum, with its sluggish water current and consequent curtailment of supplies of nitrate, of oxygen, or of carbon dioxide, must be a very different environment from the clear water pools and streams and it is not surprising to find so marked an individuality in its association of algae.

It remains to relate this upland bog on Millstone Grit with its acid waters to other waters which have been analysed in connexion with investigations of the algae or for other reasons. Pearsall (1921 b) has divided the waters of the English Lakes—and he extends his idea to other waters—into: (1) Waters with a high basic ratio  $Na + K/Ca + Mg$ . These are the waters of rocky lakes in regions of slight cultivation or none. They are very clear, very poor in nitrates and have a flora very rich in desmids. (2) Waters with a lower basic ratio. These are more cloudy as they have more sediment, are richer in nitrates and are surrounded by more cultivation and receive more sewage from inhabited places.

\* The few Heather Glen records are included in these totals.

These are rich in diatoms. There is no doubt that Miles Rough bog takes its place among those with low basic ratio and higher nitrate. The ratio Na + K/Ca + Mg is

20 April		1 June		Heather Glen	
Inlet	Outlet	Middle	Outlet	Inlet	Outlet
0.40	0.32	0.41	0.26	0.74	0.54

and is always much below 1.5, which he takes as his dividing line between the two types.\* The waters of the bog are relatively rich in nitrate. The following table shows comparative figures for nitrate content of waters from various sources. All the figures are N<sub>2</sub>O<sub>5</sub> in parts per 100,000 and are averages of the numbers of samples indicated in parenthesis;

Miles Rough bog: Inlet	1.84 (4)	Shallow wells (Thresh)	4.10 (24)
Outlet	0.85 (6)	Deep wells (Thresh)	0.44 (24)
Highest quantity in M.R. bog	2.37	River waters (Pearsall, 1921a)	0.38 (7)
Heather Glen bog: Inlet	2.80	Lake waters (silted) (Pearsall, 1921b)	0.088 (7)
Outlet	0.09	Lake waters (rocky) (Pearsall, 1921b)	0.00 (4)

River waters (Thresh, 1913)      1.11 (12)

The water entering both the bogs under investigation is therefore comparatively rich in nitrates. Its content is only exceeded by that of the shallow wells. Only in the summer months, when the nitrates are comparatively exhausted by the growth of macrophytic vegetation and of algae, do the nitrates sink to a figure at all similar to that of even the silted lakes of Pearsall's table although these belong to his nitrate-rich category.

Thresh (1913) states that vegetable matter forms very little nitrate and that nitrate is almost all due to the decay of animal matter. He found that waters from the Essex gravel beds contained from 1.56 to 5.85 parts of N<sub>2</sub>O<sub>5</sub> per 100,000, the difference being due to the extent to which the soil was manured. The fields surrounding both the bogs of the present investigation are part of grassland farms and are used for hay and pasture, the chief operation relevant to our case being the annual application of a heavy dressing of dung in the spring. This is probably the source of the nitrate and the waters take their place appropriately among the shallow well waters whose varying and comparatively rich nitrate content is probably due to cultivation and manuring of the surface soil. In this sense they are not typical sphagnum bogs, which are found in uncultivated moorland regions and are certainly practically devoid of nitrates. Pearsall (1938) shows that nitrate is almost invariably absent in the soils of moorlands and bogs. The only exceptions he gives are 'flushes' in moorland hollows, where the nitrates are carried down by drainage from adjacent grassland slopes. These provide an interesting parallel to the bog described in the present paper, though doubtless much less rich in nitrate in the absence of manuring of the surrounding soils.

I am much indebted to Prof. F. E. Fritsch for the identification of some of the algae.

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\* The calcium content is, of course, much higher than that of the English Lakes.

# THE DISSOLVED OXYGEN OF AN UPLAND POND AND ITS INFLOWING STREAM, AT YSTUMTUEN, NORTH CARDIGANSHIRE, WALES

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(*With eight Figures in the Text*)

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## I. INTRODUCTION

Pond Lluest is an area of water of about an acre in extent, situated at Ystumtu'en, a dozen miles inland from Aberystwyth, at approximately 1000 ft. above sea-level in characteristic, somewhat acid, moorland surroundings. The water is soft, containing about 6 mg./l. of calcium and very slightly acid pH 6.2-7.0. A general description of the pond, and of an inflowing stream, the Afon Tuen, including their fauna, is in the press, and will appear in the November, 1942, issue of the *Journal of Animal Ecology*. The present is a record of fifteen months' observations upon the dissolved oxygen present in the water of both the pond and the stream, during the course of which approximately 900 estimations were made, of which 816 are directly utilized.

Cyclic studies in the dissolved oxygen of fresh waters have been mainly concerned with seasonal changes in lakes and vegetation-containing rivers, and diurnal changes in the latter.

Among seasonal investigations those of Birge & Juday (1911) are notable, yielding a number of curves which include oxygen and temperature in relation to depth for Wisconsin lakes; and these have been followed by a series of studies by the same and other American workers. Clemens (1917) gives useful graphs indicating the relation between oxygen and temperature, based upon about two observations per month over a period of 9 months, for Cascadilla Creek, Ithaca, New York; he does not state the hour at which the samples were collected. Oxygen and temperature data are given for the river Wharfe by the Laboratory Staff of the West Riding Rivers Board (1930), and by Garner, Brown & Lovett (1936) for clean and polluted stations in the river Holme, Yorks. Among related

studies is that of the Thames Estuary by Butler & Coste (1923), and that of the estuary of the river Tees by Alexander, Southgate & Bassingdale (1935). Less attention has been paid to small bodies of standing fresh water; some seasonal records of dissolved oxygen, based upon one to five estimations per month, over a period of 9 months, are given by Chambers (1912) for a lagoon in the Missouri Botanical Garden at St Louis, Mo., U.S.A., and for shallow ponds by Petersen (1926) near Lake Michigan and Beattie (1930) at Farnham Royal, Bucks; none of these workers indicate the hour of the day at which the samples were collected.

The diurnal cycle had received little attention prior to the important papers of Butcher, Pentelow & Woodley (1927, 1928, 1930). Morren & Morren (1841) had shown for a fish pond in Belgium, and Chambers (1912) for the lagoon in the St Louis Botanical Garden, that considerable changes in oxygen content are associated with algal influence. Birge & Juday (1911), dealing with large bodies of standing water, fail to demonstrate any marked daily oxygen pulse in the surface waters, but were able to show one at 1-3 m. depth in Lake Mendota in September. Scott (1924) records a diurnal oxygen pulse in the surface waters of Eagle Lake, Indiana. The first work of a comprehensive character on the diurnal cycle, however, is due to Butcher, Pentelow & Woodley's study of the small, vegetation-containing, rivers Lark (polluted) and Itchen. A further contribution is made by Butcher, Longwell & Pentelow (1937, p. 38) in the course of a study of the upper waters of the river Tees in relation to sewage pollution. In France, Hubault (1927) made important observations on the diurnal cycle in the river Meurthe during the daylight hours.

It appeared to the writer that it would be interesting to compare and contrast the diurnal oxygen changes in a moorland pond containing vegetation with those of a swift mountain stream, almost devoid of vegetation, flowing into it; and also to follow the seasonal changes in more detail in a pond which was of a different character and altitude from those already investigated.

This paper is in the main concerned with cyclic studies, but it should be noted that, following the lead of Birge & Juday, Thienemann, Alsterberg and others, dissolved oxygen content is accepted as an important feature in the classification of lakes (Ström, 1928, 1930), and, as Fritsch (1931, p. 245) has pointed out, the general scheme of classification that is applied to the larger bodies should be one that is applicable to all bodies of standing water.

A useful and comparatively recent bibliography of oxygen studies concerned with fresh water is given by Welch (1935), also by Chapman (1931), and an historical introduction by Hubault (1927).

## 2. METHOD OF INVESTIGATION

An approximately weekly record, extending over 15 months, was made of the amount of dissolved oxygen in each of a series of samples taken from the stations indicated in Fig. 1. The stations, which have been described more fully by the writer in the paper referred to above, are as follows:

- A, in the *Equisetum* area.
- B, in the *Potamogeton* area.
- C, in the *Sparganium* area.
- D, in the *Scirpus* area.

- F, near the outlet, where there was no macroflora, a current flowing towards the outlet, and an insufficient accumulation of debris to hide the stones forming the bottom.  
 H, about the centre of the open water portion of the pond.  
 I, the inflowing stream (Afon Tuen) a dozen paces before its entry into the pond.

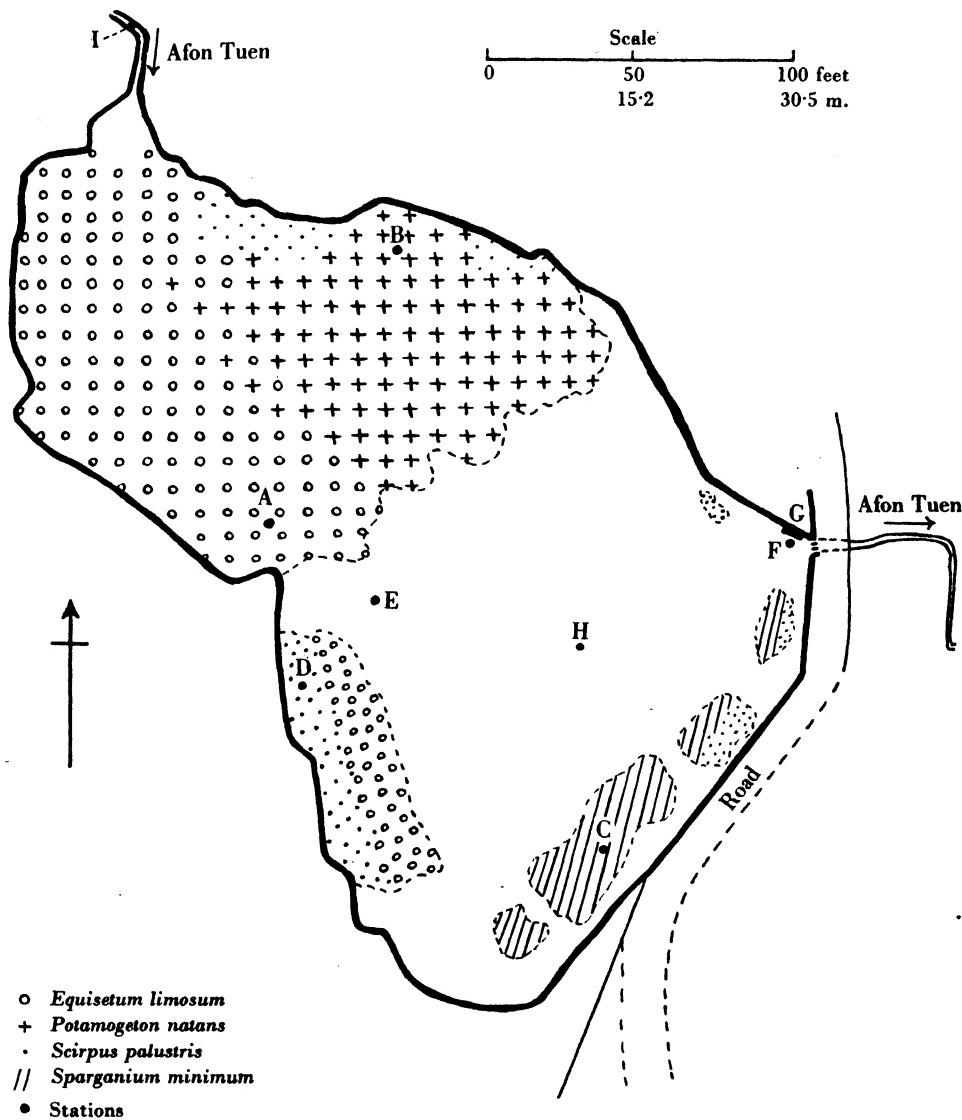


Fig. 1. Pond Lluest, Ystumtuen, indicating the distribution of the main vegetation areas, and position of stations A-I.

Except from station H the samples were obtained by wading into the water to a depth of about  $1\frac{1}{2}$  ft., and thrusting a collecting bottle some 10 in. below the surface. It is fitted with a watertight cork through which two glass tubes project; one is flush with the top of the cork and goes to the bottom of the bottle, the other is flush with the

bottom of the cork and projects about 3 in. above it. This reduces bubbling to a minimum. The distance at which the sample was taken from the bottom of the pond increased in times of flood. All the stations except H were within 2 or 3 yards of the bank. The temperature of the water was taken at the same positions, from 5 September, by a standard thermometer, by dipping it into the sample collected for oxygen estimation, the collecting bottle having been put into the pond for a short time. The air temperature, taken by the thermometer in an exposed position, was also recorded.

The water sample from station H was obtained from the bottom of the pond by the following method. A bottle, to the bottom of which a pound weight had been fastened with string, was attached to a loop in the middle of a piece of rope of sufficient length to stretch across the pond. One end of the rope was attached to a post at one end of the pond; the other was carried round to the opposite side, being held taut so that the bottle did not touch the water. The held end of the rope was then liberated and the bottle plunged into the pond. It sank rapidly, so ensuring that the sample was obtained substantially from the bottom. The sample was on all occasions free from any admixture of mud, so that the layer sampled would appear to have been just above the actual bottom, the weight keeping the bottle in an upright position and the mud not being deep. As the oxygen content of the samples from this station showed no significant difference from those obtained from the other stations, no further samples were taken after 30 December.

The dissolved oxygen was estimated by the Winkler method. The size of the samples varied from about 150 to 200 c.c. For the titration a *N*/20 sodium thiosulphate solution was used, and the oxygen calculated as milligrams oxygen per litre, rendering adjustments in relation to temperature and pressure unnecessary.

### 3. SEASONAL CYCLE

Tables 1, 2, record the oxygen and temperature data respectively from all stations, together with the pond averages, from the commencement of their systematic collection on 6 August 1940, to the end of October 1941. The seasonal data were collected during the afternoon, between 3 and 4 p.m. G.M.T., an hour which falls within the period of maximum oxygen content during the diurnal cycle in the case of the pond, and in the case of the stream during the period of minimum oxygen content.

It will be convenient to deal first with the stream data and then with the pond averages, leaving until later the examination of the differences between the several pond stations.

#### (a) *The stream*

The particulars of the oxygen and temperature of the stream are set out in Table 3, Fig. 2 giving an essentially similar graphical representation.

That the solubility of gases in water decreases with rise of temperature is a well-known fact. An inspection of Table 3 will show that a decrease in temperature as between two successive observations is almost invariably accompanied by an increase in oxygen content, and vice versa, the average relation being an oxygen difference of 0.25 mg. O<sub>2</sub>/l. for 1° C., about one-half of the deviations from this average falling between the limits of 0.1 and 0.5. Welch (1935, p. 93) gives a table indicating relation between water temperature and dissolved oxygen. He expresses the oxygen as c.c. per litre, which may be

converted into mg. per litre on the equivalence of 5·6 c.c. O<sub>2</sub> N.T.P. to 8 mg. After such conversion it may be calculated that the average oxygen difference which should be

Table 1. Record of dissolved oxygen (mg. O<sub>2</sub>/l.) from all stations

The samples of water were taken between 3 and 4 p.m. G.M.T.

	<i>Equisetum</i> (A)	<i>Potamogeton</i> (B)	<i>Scirpus</i> (D)	<i>Sparganium</i> (C)	Open water (F)	Average for pond
6 Aug. 1940	7.2	9.7	8.8	9.8	10.0	9.1
17	9.6	9.8	9.6	10.0	9.4	9.7
21	7.8	9.6	10.0	10.2	10.0	9.5
29	10.0	9.2	10.2	10.6	9.8	10.0
5 Sept.	9.0	9.0	9.4	10.0	9.2	9.3
11	9.6	10.2	10.8	10.2	10.4	10.2
18	10.0	10.0	10.4	10.2	10.2	10.2
25	10.2	10.4	10.6	10.6	10.0	10.4
1 Oct.	11.4	11.0	11.2	11.8	10.8	11.2
10	11.2	11.2	11.2	10.8	11.2	11.1
16	11.8	11.4	11.2	11.2	11.0	11.3
23	11.6	12.4	11.6	11.6	11.4	11.7
31	11.0	10.0	11.4	11.2	11.6	11.0
6 Nov.	12.0	12.0	11.8	11.8	11.8	11.9
13	12.2	12.2	12.2	12.2	12.2	12.2
27	10.4	11.6	11.8	12.1	11.8	11.5
5 Dec.	9.2	12.0	12.2	12.0	13.2	11.7
12	11.2	12.7	12.8	13.2	13.2	12.6
21	14.2	14.8	13.2	14.0	14.4	14.1
30	12.2	12.2	12.0	12.6	12.6	12.3
8 Jan. 1941	—	—	—	—	13.6	13.6
12 Feb.	12.1	12.3	11.8	12.1	11.9	12.0
26	—	—	—	—	12.9	12.9
5 Mar.	12.1	12.4	12.0	—	11.9	12.1
12	12.2	13.1	13.0	13.3	12.9	12.9
19	10.9	13.4	10.7	13.0	12.4	12.1
26	11.7	11.3	11.9	11.8	11.4	11.6
3 Apr.	12.4	12.5	12.3	12.7	12.3	12.4
9	12.6	12.7	11.8	13.0	13.1	12.6
15	11.5	11.3	11.0	11.5	11.4	11.3
23	11.2	11.6	11.2	11.2	11.1	11.3
30	12.1	12.9	11.9	12.2	12.2	12.3
7 May	11.7	12.3	11.2	11.6	11.1	11.6
15	11.2	10.6	10.5	10.6	10.6	10.7
23	9.6	10.3	10.1	10.1	10.4	10.1
28	8.7	10.3	10.7	10.4	10.2	10.1
9 June	9.4	8.7	9.9	9.7	9.5	9.4
20	9.3	8.8	9.1	8.5	8.7	8.9
29	8.0	8.6	9.1	8.9	8.7	8.7
5 July	7.7	8.1	8.8	9.2	9.1	8.6
13	5.7	6.8	6.7	7.4	6.1	6.5
19	7.4	7.9	8.8	8.5	8.2	8.2
26	7.5	8.1	8.9	8.5	8.3	8.3
2 Aug.	8.6	8.5	8.9	9.0	8.8	8.8
11	8.6	9.1	9.0	9.1	8.9	8.9
18	9.3	9.3	9.5	9.4	9.3	9.4
25	9.3	9.5	9.0	9.3	9.1	9.2
2 Sept.	8.0	8.9	9.2	9.3	9.1	8.9
9	5.9	8.0	8.5	9.1	8.5	8.0
16	9.4	9.6	9.3	9.5	9.4	9.4
23	10.3	9.8	10.0	10.9	9.8	10.2
30	9.1	9.8	9.5	9.7	9.1	9.4
7 Oct.	10.6	10.1	9.5	9.3	9.3	9.8
14	10.7	10.3	10.1	10.3	10.1	10.3
21	10.7	10.6	10.4	10.9	10.5	10.6
28	10.2	11.1	11.5	11.4	11.3	11.1

associated with 1° C. for the series of observations under present review is, assuming saturation, 0.25 mg./l. (see last column of Table 3). The close correspondence between

the observed relation and this calculated one suggests that temperature is here the essential factor in determining oxygen content.

Table 2. Record of temperature ( $^{\circ}$  C.) from all stations

The observations were made between 3 and 4 p.m. G.M.T.

	<i>Equisetum</i> (A)	<i>Potamogeton</i> (B)	<i>Scirpus</i> (D)	<i>Sparganium</i> (C)	Open water (F)	Average for pond	Air
25 Sept. 1940	10.3	—	—	—	10.2	10.2	9.9
1 Oct.	11.0	11.5	11.0	11.0	10.5	11.0	9.5
10	—	—	—	—	—	—	—
16	12.3	12.0	11.6	11.4	10.5	11.6	12.0
23	9.0	10.0	9.0	9.0	9.0	9.2	9.0
31	8.6	8.8	8.3	8.3	8.0	8.4	8.0
6 Nov.	9.0	9.0	8.0	8.5	8.5	8.6	7.1
13	6.8	7.8	6.8	6.8	6.8	7.0	5.0
27	7.0	7.0	7.3	7.0	7.0	7.1	4.0
5 Dec.	3.0	5.3	5.0	5.0	5.0	4.7	4.0
12	2.5	4.8	3.5	3.0	3.5	3.5	3.0
21	1.0	1.3	1.0	1.0	1.5	1.2	-0.3
30	6.0	6.4	6.0	6.0	6.0	6.1	8.0
8 Jan. 1941	—	—	—	—	3.0	3.0	3.5
12 Feb.	6.0	5.8	5.8	5.8	5.8	5.8	7.0
26	—	—	—	—	3.5	3.5	2.8
5 Mar.	6.0	7.0	5.0	—	5.0	5.8	5.3
12	4.0	4.8	4.0	4.3	4.5	4.3	3.0
19	9.0	8.0	6.8	7.0	6.0	7.4	11.0
26	9.2	9.5	8.0	8.5	9.0	8.8	11.0
3 Apr.	5.8	5.8	5.4	5.4	5.8	5.6	4.0
9	6.5	6.5	6.0	5.8	5.5	6.1	5.0
15	9.0	9.3	8.5	8.5	8.5	8.8	8.5
23	9.5	9.8	9.3	9.5	9.5	9.5	8.5
30	8.0	8.0	7.3	7.0	7.0	7.5	12.5
7 May	10.8	11.0	9.5	9.7	9.5	10.1	8.5
15	11.3	11.0	11.0	11.0	10.5	11.0	9.0
23	9.8	10.0	9.5	9.8	9.8	9.8	7.8
28	13.8	13.3	11.5	11.1	11.0	12.1	12.5
9 June	14.0	13.8	13.0	13.0	12.9	13.3	12.9
20	23.5	24.0	24.0	23.5	24.0	23.8	24.0
29	22.0	23.0	23.5	24.0	23.5	23.2	22.0
5 July	19.8	20.3	20.5	20.3	20.1	20.2	17.0
13	21.3	21.3	22.0	21.8	21.0	21.5	20.5
19	16.0	16.0	17.0	16.5	16.0	16.3	14.8
26	19.5	20.0	21.0	21.0	20.0	20.3	17.0
2 Aug.	20.1	20.8	22.0	21.5	21.0	21.1	21.0
11	17.0	16.7	16.0	15.8	15.9	16.3	14.0
18	17.0	17.0	16.0	16.2	15.8	16.4	15.8
25	16.5	16.2	15.0	15.1	15.0	15.6	16.0
2 Sept.	16.0	16.0	15.6	16.0	15.0	15.7	15.0
9	16.0	15.8	16.0	16.1	15.8	15.9	16.0
16	14.6	15.0	14.8	14.8	14.6	14.8	15.0
23	15.8	16.5	16.3	15.9	15.0	15.9	20.0
30	13.5	13.9	14.0	14.0	13.8	13.8	12.8
7 Oct.	14.9	15.7	14.5	13.5	13.7	14.5	18.5
14	11.7	11.9	11.0	11.3	11.0	11.4	12.5
21	12.5	12.5	11.8	12.0	11.8	12.1	11.8
28	8.7	8.8	8.4	8.0	8.2	8.4	8.0

For the greater part of the year the dissolved oxygen present is little short of saturation. But from October 1940 to January 1941 there is persistent supersaturation, and the diurnal curve for 30 September-1 October (Fig. 4) shows this condition present during almost the 24 hr. The stream, which is 6 in. to 1 ft. in depth in normal con-

ditions, falls over rock about a hundred yards higher up its course to form a small waterfall, and flows rapidly to the pond so that it has every opportunity to become well oxygenated. But Butcher *et al.* (1937, p. 40), working on the upper waters of the Tees, support by experiment their conclusion that these can become supersaturated with oxygen only as a result of photosynthesis. The present writer is as yet unable to explain this period of supersaturation in the Afon Tuen. The condition is not repeated in October 1941.

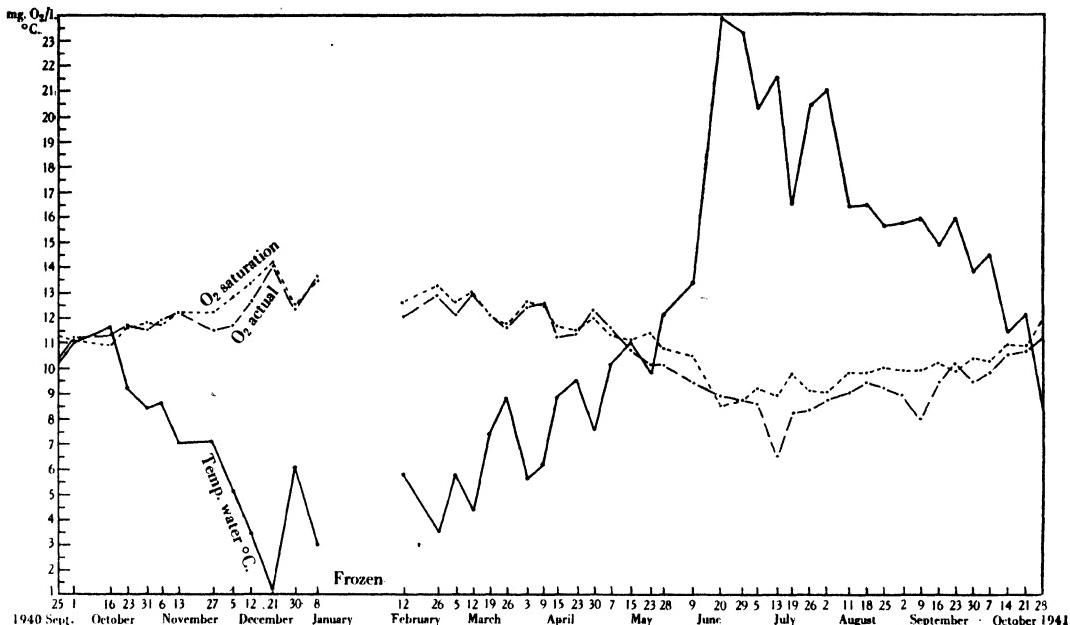


Fig. 2. Seasonal cycles in dissolved oxygen and temperature of Pond Lluest.

#### (b) *The pond*

Turning to the pond data, Table 4 and Fig. 2 record the average amount of dissolved oxygen (five stations sampled) and the average temperature, for each of the same dates as for the stream, calculated from the station records as given in Tables 1 and 2.

The result is very similar to that obtained from the stream, the correspondence between the curves representing actual and calculated oxygen being very close. Occasional slight supersaturation occurs, but the persisting supersaturation shown by the stream from October to January does not occur in the pond; saturation is for the most part less than 100%, though the samples were collected during the period in the diurnal cycle when photosynthesis was exerting its maximum effect.

The general similarity between the oxygen curves for pond and stream is so considerable that it appears useful to compare them in detail in terms of their percentage saturation values. This is done in Table 5, which is graphed in Fig. 3. The number of hours of sunshine at Ystumtuen is also included, calculated from the official records for Aberystwyth by Glasspoole & Hancock's method (1936).

It will be noted how relatively close to full saturation both oxygen curves remain throughout the year, but how rarely a condition of supersaturation is reached. In the

stream, as already mentioned, this only occurs during the latter part of 1940, when it approximates 108; it is not repeated in October 1941. In the pond the slight supersaturation occasionally reached is sporadic. Both curves fluctuate round about 96% of

Table 3. *Dissolved oxygen and temperature of the stream*

The samples of water were obtained and their temperature taken between 3 and 4 p.m. G.M.T.

Date	Temp. of water °C.	Actual	Saturation calculated from temp.	Difference between actual and saturation	Difference between successive dates		
					Temp. °C.	Oxygen (actual)	Oxygen (saturation)
1 Oct. 1940	11.5	11.8	11.0	0.8	—	—	—
16	11.3	12.4	11.0	1.4	-0.2	0.6	0.0
23	9.9	12.4	11.4	1.0	-1.4	0.0	0.4
31	8.5	12.6	11.8	0.8	-1.4	0.2	0.4
6 Nov.	8.5	12.8	11.8	1.0	0.0	0.2	0.0
13	7.0	13.2	12.2	1.0	-1.5	0.4	0.4
27	6.0	13.6	12.5	1.1	-1.0	0.4	0.3
5 Dec.	5.5	13.6	12.6	1.0	-0.5	0.0	0.1
12	4.8	14.0	12.9	1.1	-0.7	0.4	0.3
21	1.8	14.0	13.9	0.1	-3.0	0.0	1.0
30	6.0	13.2	12.5	0.7	4.2	-0.8	-1.4
8 Jan. 1941	3.3	13.8	13.4	0.4	-2.7	0.6	0.9
12 Feb.	6.3	11.8	12.4	-0.6	3.0	-2.0	-1.0
26	3.0	12.9	13.5	-0.6	-3.3	1.1	1.1
5 Mar.	6.5	11.7	12.3	-0.6	3.5	-1.2	-1.2
12	5.0	12.6	12.8	-0.2	-1.5	0.9	0.5
19	8.5	11.8	11.8	0.0	3.5	-0.8	-1.0
26	9.0	11.5	11.6	-0.1	0.5	-0.3	-0.2
3 Apr.	5.5	12.1	12.7	-0.6	-3.5	0.6	1.1
9	7.3	11.5	12.1	-0.6	1.8	-0.6	-0.6
15	9.0	11.0	11.6	-0.6	1.7	-0.5	-0.5
23	10.0	11.0	11.3	-0.3	1.0	0.0	-0.3
30	11.0	10.5	11.1	-0.6	1.0	-0.5	-0.2
7 May	10.0	11.0	11.3	-0.3	-1.0	0.5	0.2
15	9.3	10.7	11.5	-0.8	-0.7	-0.3	0.2
23	9.5	10.6	11.5	-0.9	0.2	-0.1	0.0
28	11.0	10.7	11.1	-0.4	1.5	0.1	-0.4
9 June	12.8	10.0	10.6	-0.6	1.8	-0.7	-0.5
20	24.0	8.0	8.5	-0.5	11.2	-2.0	-2.1
29	24.8	7.9	8.4	-0.5	0.8	-0.1	-0.1
5 July	20.0	8.7	9.2	-0.5	-4.8	0.8	0.8
13	20.5	7.9	9.1	-1.2	0.5	-0.8	-0.1
19	16.3	9.3	9.8	-0.5	-4.2	1.4	0.7
26	19.3	8.6	9.3	-0.7	3.0	-0.7	-0.5
2 Aug.	22.0	8.4	8.8	-0.4	2.7	-0.2	-0.5
11	16.3	9.1	9.8	-0.7	-5.7	0.7	1.0
18	16.4	9.3	9.8	-0.5	0.1	0.2	0.0
25	16.0	9.3	9.9	-0.6	-0.4	0.0	0.1
2 Sept.	15.7	9.6	9.9	-0.3	-0.3	0.3	0.0
9	15.5	9.8	10.0	-0.2	-0.2	0.2	0.1
16	14.4	9.9	10.3	-0.4	-1.1	0.1	0.3
23	16.5	9.6	9.8	-0.2	2.1	-0.3	-0.5
30	13.1	10.2	10.6	-0.4	-3.4	0.6	0.8
7 Oct.	15.0	9.9	10.1	-0.2	1.9	-0.3	-0.5
14	11.9	10.5	10.8	-0.3	-3.1	0.6	0.7
21	11.5	10.6	10.9	-0.3	-0.4	0.1	0.1
28	9.0	11.2	11.6	-0.4	-2.5	0.6	0.7
Average (neglecting sign)				0.56	2.05	0.52	0.52
Inverse ratio					1.0	0.25	0.25

saturation during the greater part of the year, with a tendency to be a little lower from May to September than at other times. During the same period, the week to week fluctuations of the pond curve are much more considerable than those for the stream. It will be seen that they are associated with fluctuations of the sunshine curve, and that

of the three days upon which supersaturation is attained during the period, two were very sunny, and the other moderately so, and that the two lowest saturation records, which are also the lowest of the whole series, are associated with low sunshine. Throughout

Table 4. *Dissolved oxygen and temperature averages for the pond*

The samples of water were obtained and their temperature taken between 3 and 4 p.m. G.M.T.

Date	Average temp. of water °C.	Average mg. O <sub>2</sub> /l.			Difference between successive dates		
		Actual	Saturation calculated from temp.	Difference between actual and saturation	Temp.. °C.	Oxygen (actual)	Oxygen (saturation)
25 Sept. 1940	10.2	10.4	11.3	-0.9	—	—	—
1 Oct.	11.0	11.2	11.1	0.1	0.8	0.8	-0.2
16	11.6	11.3	10.9	0.4	0.6	0.1	-0.2
23	9.2	11.7	11.6	0.1	-2.4	0.4	0.7
31	8.4	11.5	11.8	-0.3	-0.8	-0.2	0.2
6 Nov.	8.6	11.9	11.7	0.2	0.2	0.4	-0.1
13	7.0	12.2	12.2	0.0	-1.6	0.3	0.5
27	7.1	11.5	12.2	-0.7	0.1	-0.7	0.0
5 Dec.	5.1	11.7	12.8	-1.1	-2.0	0.2	0.6
12	3.5	12.6	13.3	-0.7	-1.6	0.9	0.5
21	1.2	14.1	14.2	-0.1	-2.3	1.5	0.9
30	6.1	12.3	12.5	-0.2	4.9	-1.8	-1.7
8 Jan. 1941	3.0	13.6	13.5	0.1	-3.1	1.3	1.0
12 Feb.	5.8	12.0	12.6	-0.6	2.8	-1.6	-0.9
26	3.5	12.9	13.3	-0.4	-2.3	0.9	0.7
5 Mar.	5.8	12.1	12.6	-0.5	2.3	-0.8	-0.7
12	4.3	12.9	13.0	-0.1	-1.5	0.8	0.4
19	7.4	12.1	12.1	0.0	3.1	-0.8	-0.9
26	8.8	11.6	11.7	-0.1	1.4	-0.5	-0.4
3 Apr.	5.6	12.4	12.6	-0.2	-3.2	0.8	0.9
9	6.1	12.6	12.5	0.1	0.5	0.2	-0.1
15	8.8	11.2	11.7	-0.5	2.7	-1.4	-0.8
23	9.5	11.3	11.5	-0.2	0.7	0.1	-0.2
30	7.5	12.3	12.0	0.3	-2.0	1.0	0.5
7 May	10.1	11.6	11.3	0.3	2.6	-0.7	-0.7
15	11.0	10.7	11.1	-0.4	0.9	-0.9	-0.2
23	9.8	10.1	11.4	-1.3	-1.2	-0.6	0.3
28	12.1	10.1	10.8	-0.7	2.3	0.0	-0.6
9 June	13.3	9.4	10.5	-1.1	1.2	-0.7	-0.3
20	23.8	8.9	8.5	0.4	10.5	-0.5	-2.0
29	23.2	8.7	8.7	0.0	-0.6	-0.2	0.2
5 July	20.2	8.6	9.2	-0.6	-3.0	-0.1	0.5
13	21.5	6.5	8.9	-2.4	1.3	-2.1	-0.3
19	16.3	8.2	9.8	-1.6	-5.2	1.7	0.9
26	20.3	8.3	9.1	-0.8	4.0	0.1	-0.7
2 Aug.	21.0	8.8	9.0	-0.2	0.7	0.5	-0.1
11	16.3	9.0	9.8	-0.8	-4.7	0.2	0.8
18	16.4	9.4	9.8	-0.4	0.1	0.4	0.0
25	15.6	9.2	10.0	-0.8	-0.8	-0.2	0.2
2 Sept.	15.7	8.9	9.9	-1.0	0.1	-0.3	-0.1
9	15.9	8.0	9.9	-1.9	0.2	-0.9	0.0
16	14.8	9.4	10.2	-0.8	-1.1	1.4	0.3
23	15.9	10.2	9.9	0.3	1.1	0.8	-0.3
30	13.8	9.4	10.4	-1.0	-2.1	-0.8	0.5
7 Oct.	14.5	9.8	10.3	-0.5	0.7	0.4	-0.1
14	11.4	10.3	10.9	-0.6	-3.1	0.5	0.6
21	12.1	10.6	10.8	-0.2	0.7	0.3	-0.1
28	8.4	11.1	11.8	-0.7	-3.7	0.5	1.0
		Average (neglecting sign)	0.56	2.02	0.69	0.51	
		Inverse ratio		1.0	0.34	0.25	

the whole period of the observations the highest saturation recorded for the pond was 105% and on only three occasions was it less than 90%.

A seasonal curve for dissolved oxygen is given by Petersen (1926) for a shallow pond

*A biological study of an upland pond*

near Lake Michigan. It is of the same general type as the Pond Lluest curve, but higher in winter and lower in summer, and its highest and lowest points are both about a month later. The more intense frost in Wisconsin and the high evaporation in summer introduce disturbing features which are not present under the Ystumtuen conditions. Petersen also gives a temperature curve, but the correlation between this and his oxygen curve is much less close than at Pond Lluest. From September to the beginning of January

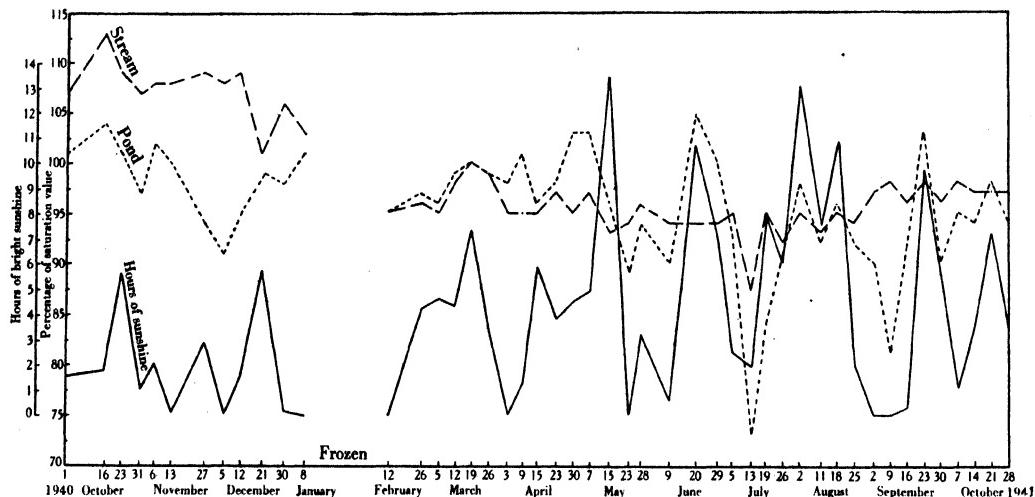


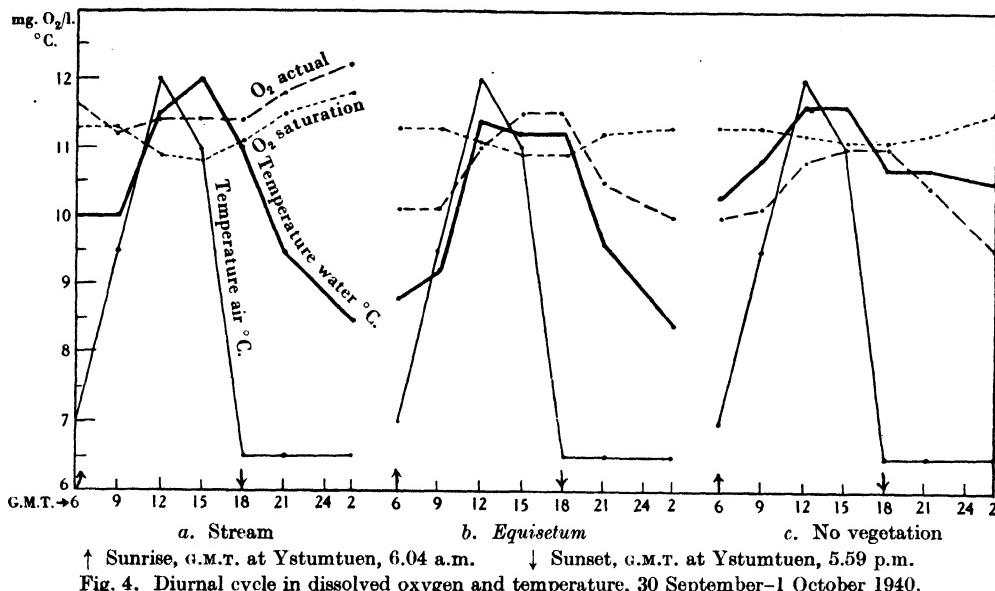
Fig. 3. Seasonal variations in (a) the amount of dissolved oxygen in the water of Pond Lluest and of the Afon Tuen, expressed as percentage of saturation value, and (b) the number of hours of bright sunshine.

Table 5. Seasonal variations in (a) the amount of dissolved oxygen in the water of Pond Lluest and of the Afon Tuen, expressed as percentage of saturation value, and (b) the number of hours of bright sunshine

Date 1940-1	Saturation value %				Hours of bright sun- shine	Date 1941	Saturation value %				Hours of bright sun- shine
	Differences		Stream higher	Pond higher			Differences		Stream higher	Pond higher	
	Stream	Pond					Stream	Pond			
1 Oct.	107	101	6	—	1·6	7 May	97	103	—	6	4·9
16	113	104	9	—	1·8	15	93	96	—	3	13·5
23	109	101	8	—	5·7	23	94	89	5	—	0·0
31	107	97	10	—	1·0	28	96	94	2	—	3·2
6 Nov.	108	102	6	—	2·1	9 June	94	90	4	—	0·5
13	108	100	8	—	0·1	20	94	105	—	11	10·7
27	109	94	15	—	2·9	29	94	100	—	6	6·9
5 Dec.	108	91	17	—	0·0	5 July	95	93	2	—	2·5
12	109	95	14	—	1·6	13	87	73	14	—	1·9
21	101	99	2	—	5·8	19	95	84	11	—	7·9
30	106	98	8	—	0·2	26	92	91	1	—	6·0
8 Jan.	103	101	2	—	0·0	2 Aug.	95	98	—	3	13·1
12 Feb.	95	95	—	—	0·0	11	93	92	1	—	7·5
26	96	97	—	1	4·2	18	95	96	—	1	10·9
5 Mar.	95	96	—	1	4·6	25	94	92	2	—	2·0
12	98	99	—	1	4·3	2 Sept.	97	90	7	—	0·0
19	100	100	—	—	7·3	9	98	81	17	—	0·0
26	99	99	—	—	3·5	16	96	92	4	—	0·3
3 Apr.	95	98	—	3	0·0	23	98	103	—	5	9·8
9	95	101	—	6	1·3	30	96	90	6	—	5·5
15	95	96	—	1	5·9	7 Oct.	98	95	3	—	1·0
23	97	98	—	1	3·8	14	97	94	3	—	3·4
30	95	103	—	8	4·5	21	97	98	—	1	7·2
					28	97	94	3	—	3·5	

there is, as in Pond Lluest, a falling temperature associated with rising oxygen, but in April and May rising temperature is accompanied by steady oxygen, and during June, July and August, falling oxygen (from the highly supersaturated level of 10 cc./l., i.e. 14.2 mg./l., to the much undersaturated level of 1 c.c./l., i.e. 1.3 mg./l.) is associated with a relatively constant temperature fluctuating between 20° C. (saturation 9.2 mg./l.) and 25° C. (saturation 5.4 mg./l.). During this period of falling oxygen, the water, normally about 2 ft. in depth, steadily sinks to about 6 in. Petersen does not record the hour at which his observations were taken.

Beattie (1930) gives seasonal oxygen curves for six mosquito ponds near Farnham Royal, Bucks, each based upon an average of about one record per month. The ponds are shallow and show a tendency to dry up during the hot weather. The general form



↑ Sunrise, G.M.T. at Ystumtuen, 6.04 a.m. ↓ Sunset, G.M.T. at Ystumtuen, 5.59 p.m.  
Fig. 4. Diurnal cycle in dissolved oxygen and temperature, 30 September–1 October 1940.

of the curves, that is to say the fall in spring, the lowness in summer, and the rise in autumn, is in harmony with the Pond Lluest curves, though there is a dramatic drop in January, when the ponds were covered with ice. The quantity of dissolved oxygen is, however, strikingly different from that in Pond Lluest, and the curve for percentage saturation values presents a very different appearance. The writer's calculations based upon Beattie's temperature and oxygen data for Baker's Pond, for example, will make this clear:

Date	Temp. °C. (Beattie)	c.c. O₂/l. (Beattie)	mg. O₂/l. (E.M.O.L.)	Saturation mg. O₂/l. (E.M.O.L.)	% of saturation value (E.M.O.L.)
6 Mar.	9	6	8.6	11.6	74
30 Apr.	9	5	7.1	11.6	61
2 May	16	3	4.3	9.9	43
25 June	20	1	1.4	9.2	15
11 July	22	1	1.4	8.8	16
16 July	20	1	1.4	9.2	15
23 July	22	1	1.4	8.8	16
17 Sept.	14	0.2	0.3	10.4	3
24 Oct.	9	3	4.3	11.6	37
27 Nov.	8	5	7.1	11.9	60
17 Dec.	3	6	8.6	13.5	64
28 Jan.	0	1.5	2.0	13.8	14

Beattie states that the temperature readings were taken at different times on different days, but making all allowance for this there would seem to be a considerable difference between the Farnham Royal and Ystumtuen ponds. There is a considerable amount of decomposing organic matter in the former, so that the relative influence of air and decomposing organic matter is evidently very different from Pond Lluest, the depleting agents gaining the upper hand at Farnham Royal, and the air at Pond Lluest.

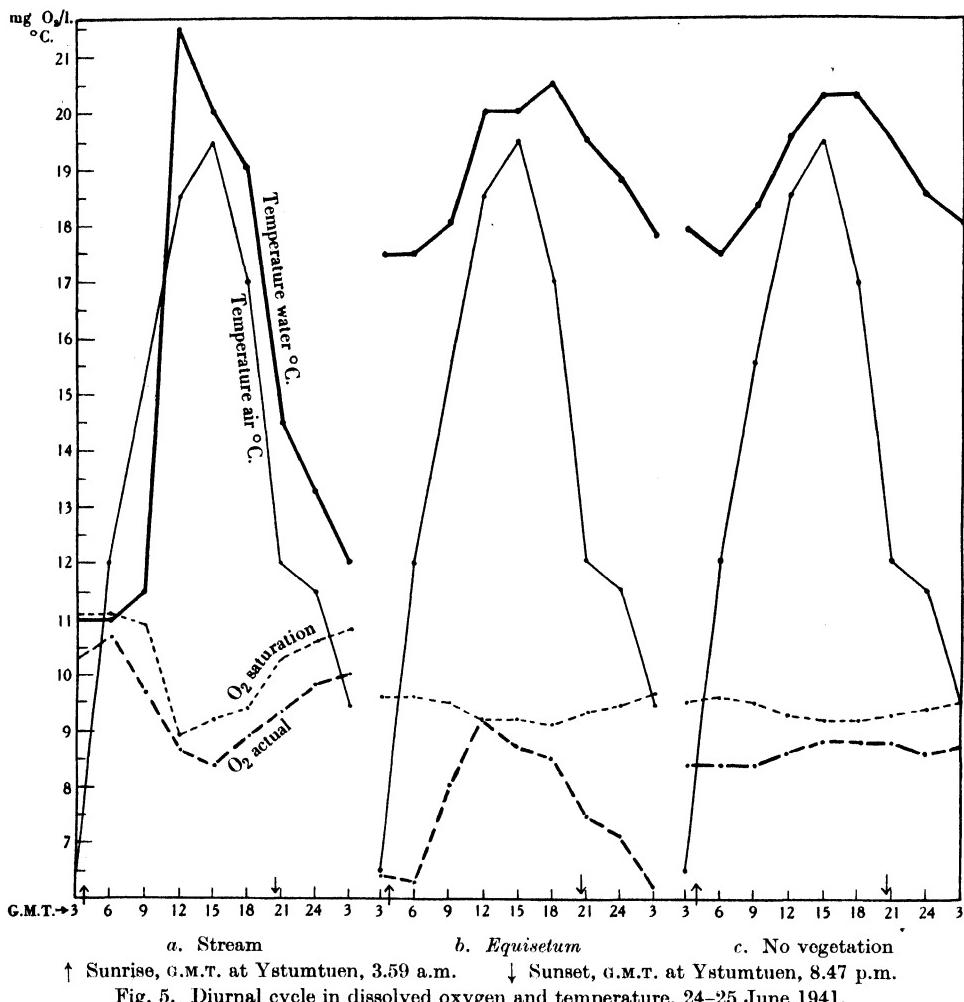


Fig. 5. Diurnal cycle in dissolved oxygen and temperature, 24–25 June 1941.

The dramatic drop in oxygen content at Farnham Royal in January, when contact with the air was prevented by ice, follows naturally, whereas the fall at Ystumtuen would be expected to be very much less, partly on account of the smaller amount of decomposing matter, and also because of the water movement associated with the through-flowing current, even though this may be very slight in places.\*

\* On 19 February 1942, when the pond was largely frozen over, a sample of water from below 1½ in. of ice at the *Equisetum* station, and another from under 2½ in. of ice at the *Potamogeton* station, were both found to contain 14·1 mg. O<sub>2</sub>/l. (being 98% of saturation); and a sample from under 1 in. of ice at the open-water station near the outlet, contained 14 mg. O<sub>2</sub>/l. (97% of saturation). In all three cases the temperature was 0·5° C. (air temperature -4°). A central patch amounting to about one-eighth of the open water remained unfrozen in the open-water half of the pond. This had been the condition of the pond for 4 days.

On the other hand, it is clear from the work of Butcher *et al.* (1927, 1928, 1930) on the diurnal oxygen changes in the rivers Lark and Itchen, that the seasonal curves for these rivers, constructed from the diurnal maxima, show, during the season when green plants are active, much higher values than Pond Lluest, photosynthesis being much more effective. This is especially the case in the Lark, where supersaturation is present from February to August and reaches as much as 181 %. Further comparison is made with these rivers subsequently (p. 373).

A closer approximation to the Afon Tuen curve is made by the curve given by Clemens (1917) for Cascadilla Creek, Ithaca, New York, where saturation does not deviate very greatly from 100 % throughout the 9 months of the investigation, from December to August; also by the values found by the Laboratory Staff of the West Riding Rivers Board (1930) for their Ulleskelf station in the River Wharfe, and by the curve given by Garner *et al.* (1936) for their unpolluted station 1, on the river Holme, Yorks, and by Butcher *et al.* (1937) for unpolluted stations in the upper reaches of the river Tees. In the first two of these investigations the time of day at which the samples were taken is not given, and in the last the hour is in general about 10.45 a.m. In none of the three cases are diurnal changes given.

#### 4. DIURNAL CYCLE

Observations were made at approximately 3-hourly intervals over periods of 24 hr., on 30 September-1 October 1940, 21-22 December 1940, and 24-25 June 1941. The results are given in Tables 6-8 and Figs. 4 and 5. Each record of dissolved oxygen is the average of two estimations. The scale of hours is G.M.T.; the times of sunrise and sunset are G.M.T. at Ystumtuen. Less complete data were collected on other occasions (Table, p. 372).

##### (a) *The stream*

The graphs (Figs. 4, 5), in addition to recording the oxygen cycle, give also the temperature cycles of the air and the water. They also include, as in Fig. 2, a curve representing the theoretical oxygen values to be associated with the observed temperatures, assuming saturation. The December graphs are omitted as no significant variation in oxygen saturation was observed. In the summer data the air temperature reaches its highest point at noon, and that of the water, showing a time lag, is highest at 3 p.m. The most significant feature is, however, the inverse relation between oxygen and temperature, and the parallelism between the curves representing actual and calculated oxygen content respectively. Temperature would thus appear to be the essential factor in the determination of the diurnal oxygen cycle of the stream, as has already been seen to be the case for the seasonal cycle.

The September curve suggests (except for the 9 a.m. record) that the condition of supersaturation, noted above in the seasonal curve over this period, is a continuous phenomenon diurnally as well as seasonally. In June the oxygen content is a little below saturation. This type of oxygen curve, highest at night and lowest during the afternoon, forms the end-term of a lentic series related to vegetation conditions. Butcher *et al.* (1930), reviewing their researches into diurnal changes in the dissolved oxygen of river waters, find that all the streams they have examined show curves of the type to be recorded later for Pond Lluest, in which the contrast is between afternoon peaks and night troughs. The degree of the contrast, however, varies much; it is most during the period of the diatom maximum in the river Lark, less, though still very appreciable, in

Table 6. *Diurnal cycle, 30 September-1 October 1940*

Sunrise, G.M.T. at Ystumtuen: 6.04 a.m. Sunset, G.M.T. at Ystumtuen: 5.59 p.m.

G.M.T.	...	6 a.m.	9 a.m.	12 noon	3 p.m.	6 p.m.	9 p.m.	2 a.m.
Dissolved oxygen mg./l.								
Stream		11.6	11.2	11.4	11.4	11.4	11.8	12.2
Pond ( <i>Equisetum</i> )		8.8	9.2	11.4	11.2	11.2	9.6	8.4
Pond (no vegetation)		10.3	10.8	11.6	11.6	10.7	10.7	10.5
Temp. °C.								
Stream		10.0	10.0	11.5	12.0	11.0	9.5	8.5
Pond ( <i>Equisetum</i> )		10.1	10.1	11.0	11.5	11.5	10.5	10.0
Pond (no vegetation)		10.0	10.1	10.5	11.0	11.0	10.5	9.5
Air		7.0	9.5	12.0	11.0	6.5	6.5	6.5
Dissolved oxygen at saturation mg./l.								
Stream		11.3	11.3	10.9	10.8	11.1	11.5	11.8
Pond ( <i>Equisetum</i> )		11.3	11.3	11.1	10.9	10.9	11.2	11.3
Pond (no vegetation)		11.3	11.3	11.2	11.1	11.1	11.2	11.5
Dissolved oxygen, percentage of saturation value								
Stream		103	99	105	106	103	103	103
Pond ( <i>Equisetum</i> )		78	81	103	103	103	86	74
Pond (no vegetation)		91	96	104	105	96	96	91

Table 7. *Diurnal cycle, 21-22 December 1940*

Sunrise, G.M.T. at Ystumtuen: 8.25 a.m. Sunset, G.M.T. at Ystumtuen: 4.03 p.m.

G.M.T.	... 12 noon	3 p.m.	6 p.m.	10 p.m.	2 a.m.	6 a.m.	9 a.m.	12 noon
Dissolved oxygen mg./l.								
Stream	13.9	14.0	13.9	14.0	13.9	13.9	14.3	13.9
Pond ( <i>Equisetum</i> )	13.8	14.2	14.2	14.0	14.4	14.7	14.7	14.5
Pond (no vegetation)	14.2	14.2	14.0	14.0	14.0	14.2	14.4	14.2
Temp. °C.								
Stream	2.0	1.8	1.3	1.3	1.3	1.3	1.3	1.8
Pond ( <i>Equisetum</i> )	1.5	1.5	1.0	0.8	0.5	0.5	0.5	0.5
Pond (no vegetation)	1.5	1.5	1.3	1.0	0.8	0.8	0.8	1.0
Air	0.0	-0.3	-0.5	-0.5	-2.0	-2.0	-2.0	-1.5
Dissolved oxygen at saturation mg./l.								
Stream	13.8	13.9	14.1	14.1	14.1	14.1	14.1	13.9
Pond ( <i>Equisetum</i> )	14.0	14.0	14.2	14.3	14.4	14.4	14.4	14.4
Pond (no vegetation)	14.0	14.0	14.1	14.2	14.3	14.3	14.3	14.2
Dissolved oxygen, percentage of saturation value								
Stream	101	101	99	99	99	99	101	100
Pond ( <i>Equisetum</i> )	99	101	100	98	100	102	102	101
Pond (no vegetation)	101	101	99	99	98	99	101	100

Table 8. *Diurnal cycle, 24-25 June 1941*

Sunrise, G.M.T. at Ystumtuen: 3.59 a.m. Sunset, G.M.T. at Ystumtuen: 8.47 p.m.

G.M.T.	... 3 a.m.	6 a.m.	9 a.m.	12 noon	3 p.m.	6 p.m.	9 p.m.	12 m.n.	3 a.m.
Dissolved oxygen mg./l.									
Stream	10.3	10.7	9.7	8.7	8.4	8.9	9.3	9.8	10.0
Pond ( <i>Equisetum</i> )	6.4	6.3	8.0	9.2	8.7	8.5	7.5	7.1	6.3
Pond (no vegetation)	8.4	8.4	8.4	8.6	8.8	8.8	8.8	8.6	8.7
Temp. ° C.									
Stream	11.0	11.0	11.5	21.5	20.0	19.0	14.5	13.3	12.0
Pond ( <i>Equisetum</i> )	17.5	17.5	18.0	20.0	20.0	20.5	19.5	18.8	17.8
Pond (no vegetation)	18.0	17.5	18.3	19.5	20.3	20.3	19.5	18.5	18.0
Air	6.5	12.0	15.5	18.5	19.5	17.0	12.0	11.5	9.5
Dissolved oxygen at saturation mg./l.									
Stream	11.1	11.1	10.9	8.9	9.2	9.4	10.3	10.6	10.8
Pond ( <i>Equisetum</i> )	9.6	9.6	9.5	9.2	9.2	9.1	9.3	9.4	9.6
Pond (no vegetation)	9.5	9.6	9.5	9.3	9.2	9.2	9.3	9.4	9.5
Dissolved oxygen, percentage of saturation value									
Stream	93	96	89	98	91	95	90	92	93
Pond ( <i>Equisetum</i> )	67	66	84	100	95	93	81	76	66
Pond (no vegetation)	88	88	88	92	96	96	95	91	92

the period of larger plant maximum in the Lark, and but slight in the river Tern, a stream with relatively poor flora. They point out that in a stream without vegetation the times of the troughs and peaks should be reversed. This is actually the case in the Afon Tuen. The only comparable recorded instance known to the writer is that of the river Meurthe close to its source, at Rudlin in the Hautes Vosges, for which Hubault (1927, p. 52) published observations made during the hours of daylight in mid-September.

(b) *The pond*

Turning to the graphs (Figs. 4*b*, *c*; 5*b*, *c*), representing the equivalent data for the pond, an entirely different picture is presented. The observations were confined to stations A and F, the former in an area of congested *Equisetum* growth, and the latter in a patch of open water free from macrovegetation. As the records for September and June are more easily interpreted than those for December they will be considered first. The curves based upon them are generally similar, their features more pronounced in those for the *Equisetum* area. It will be seen from the September *Equisetum* graph (Fig. 4*b*) that instead of the oxygen varying inversely as the temperature, it now varies directly with it. The highest oxygen is from 3 to 6 p.m.; from here it falls rapidly to a low period during the night. Reference to the saturation curve indicates that for a period from about noon to 6.30 p.m. the oxygen is greater than anticipation based on temperature, while with reduced light intensity towards sunset and during the night, the photosynthetic activity ceasing, the effect of the respiratory absorption of oxygen by both plant and animal makes itself obvious, and the amount of oxygen falls rapidly a good deal below anticipation based on temperature. Daylight is followed, after a time lag, by plant liberation of oxygen once again, and this proceeds to gain over respiratory absorption during the morning, until at about noon the water becomes supersaturated. The effect of plant activity is thus to lead to an oxygen curve which runs inversely to that for the stream. A reflexion of this relation, in less marked terms, is found in the open water area, the records from which are graphed in Fig. 4*c*, and this in spite of the fact that the water is free from macrovegetation. This is to be explained, apart from any influence green algae may be exerting (which does not appear to be material for the station and period in question), by water circulation, the flow being from areas of rich vegetation towards this open area which is situated close to the outlet. Similar remarks apply to the records for 24–25 June.

The corresponding observations for December show no significant changes in oxygen saturation following the dying down of the macrovegetation. At the time of sampling, there was a strong, most biting, north-easterly wind, with rapid freezing of the pond on the *Equisetum* side. The ice, which was absent from the greater part of the pond, including the open water station, had increased overnight at the *Equisetum* station from a film to three-quarters of an inch in thickness by 6 a.m., and had to be broken before wading in to take the sample.

In terms of percentage saturation the 30 September–1 October *Equisetum* curve rises from a night minimum of 74% to a day maximum of 103%, and the corresponding percentages for 24–25 June are 66 and 100; for 21–22 December there is no appreciable difference in percentage saturation between day and night, the values fluctuating closely about 100.

Figs. 6 and 7, covering the periods 10–16 September and 11–16 October, include curves

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which illustrate further the characteristic form of the diurnal oxygen curve in the *Equisetum* region of the pond, the inverse relation between the curve representing actual oxygen and the saturation figures based on temperature readings, and the way in which temperature effects are masked by photosynthetic influences.

The above, together with estimations made at certain other times from individual stations, mostly the *Equisetum* station, in addition to the routine series, are collected below in fuller illustration of diurnal variation.

6 a.m. G.M.T. (except items marked * which are 7 a.m.)				3 p.m. G.M.T. (except items marked * which are noon)			
		mg. O <sub>2</sub> /l.	Satura-tion value %		mg. O <sub>2</sub> /l.	Satura-tion value %	Temp. °C.
	1940						
<i>Equisetum</i>	30 Sept.	8.8	11.3	78	10.1	11.2	10.9
Open water	30	10.3	11.3	91	10.0	11.6	11.1
<i>Equisetum</i>	21 Dec.	—	—	—	—	14.2	14.0
	22	15.1	14.3	106	0.8	—	—
Open water	21	—	—	—	—	14.4	14.0
	22	14.2	14.2	100	1.0	—	—
1941							
<i>Equisetum</i>	24 June	6.3	9.6	66	17.5	8.7*	9.2*
Open water	24	8.4	9.6	88	17.5	8.8	9.2
Open water	13 July	6.7	9.2	73	20.0	7.0	9.0
	14	6.1	9.4	65	18.7	7.1	9.2
<i>Scirpus</i>	13	5.0	9.2	54	20.0	6.8	9.0
	14	6.3	9.4	67	18.7	6.9	9.2
<i>Sparganium</i>	14	6.1	9.4	65	18.5	—	—
<i>Potamogeton</i>	14	5.3	9.4	56	18.5	—	—
<i>Equisetum</i>	(1) 13	3.0	9.1	33	20.4	5.7	8.9
	(2) 14	3.1	9.4	33	19.0	6.4	9.2
Adjoining	(3) 2 Aug.	—	—	—	—	8.7	9.1
<i>Equisetum</i>	3	6.4	9.4	68	18.5	8.6	9.2
	4	5.0	9.4	53	18.3	—	—
Open water	(4) 2	—	—	—	—	8.7	9.1
	3	7.3	9.4	78	18.7	8.7	9.2
	4	6.7	9.4	71	18.3	—	—
<i>Equisetum</i>	10 Sept.	—	—	—	—	6.5	10.0
	11	4.3	10.1	43	14.8	6.8	10.0
	12	5.3	10.3	51	14.3	8.8	10.1
	13	6.5	10.4	63	14.0	10.6	10.1
	14	7.2	10.4	69	14.0	10.0	10.0
	15	7.0	10.4	67	13.7	9.6	10.3
	16	5.6	10.6	53	13.0	10.7	9.9
	18	—	—	—	—	10.2	10.0
	19	6.7	10.5	64	13.3	8.1	10.6
	20	6.5*	10.7*	61*	12.5*	8.9	10.6
	23	—	—	—	—	10.3	9.9
	24	7.4*	10.4*	71*	14.0*	11.2	9.9
	25	8.0	10.0	80	15.5	9.8	9.9
	26	6.5	10.1	64	15.2	8.2	9.9
	27	6.0	10.1	59	15.0	—	—
	30	—	—	—	—	9.1	10.5
11 Oct.	—	—	—	—	—	9.9	10.3
	12	9.7*	11.2*	87*	10.5*	10.5	10.7
	13	7.3*	11.2*	65*	10.4*	10.8	11.1
	14	7.5*	11.1*	68*	10.9*	10.1	11.1
	15	7.1*	11.3*	63*	10.1*	10.0	11.1
	16	8.2*	11.1*	74*	11.1*	10.7	10.6
	19	—	—	—	—	10.0	10.7

(1) Noon: mg. O<sub>2</sub>/l. 6.0; saturation 8.9; % saturation 67; temp. 21.5°C.

(2) Noon: " 6.3 " 9.3; " 68; " 19.5°C.

(3) 8.30 p.m.: " 8.1; " 9.2; " 88; " 20.0°C.

(4) 8.30 p.m.: " 8.6; " 9.2; " 93; " 20.0°C.

The tendency for the *Equisetum* percentage saturation maxima to fall occasionally to relatively low values is in keeping with their action in the weekly records. The occasional falls in its percentage saturation minima, notably on 13 and 14 July and on 11 September 1941, are also noteworthy.

The striking effect of the activity of green plants, particularly algae, in producing diurnal variations in the amount of dissolved oxygen in small bodies of standing water, has been shown by Morren & Morren (1841), and by Chambers (1912), and a diurnal pulse, though elusive for many of the larger bodies of standing water, has been shown by Birge & Juday (1911) at a depth of 1-3 m., in Lake Mendota, due to algae, and by Scott (1924) for the surface waters, both pelagic and littoral, of Eagle Lake, Indiana. But our knowledge of the diurnal pulse in freshwaters is in the main due to the work upon rivers undertaken by Butcher *et al.* (1927, 1928, 1930). These investigators give diurnal oxygen curves for the rivers Lark and Itchen, taken at approximately monthly intervals over a year. These show a markedly greater effect of plant activity than do those for Pond Lluest, particularly in the case of the Lark for the period from March to May, when a saturation range from 36 to 181 % over a period of 24 hr. is recorded, with as much as 10 hr. at over 100 %. This high diurnal variation was coincident with the maximum growth of diatoms, which were very numerous then in the bed of the river. After the diatoms had decreased almost to disappearance the larger plants attained their maximum influence, in June, leading to an oxygen saturation of 124 %. In the Lark diurnal saturation maxima exceed 100 % from February to August. In the Itchen, with few diatoms, the high spring values are not attained, but at the time of the larger plant maximum the values reached are comparable with those for the Lark, thus on 27-28 July the percentage saturation ranges from 68 to 126. It has been seen from the seasonal curve representing diurnal saturation maxima (averaging five stations) for Pond Lluest (Figs. 2, 3), that these vary little throughout the year and are ordinarily a little less than 100 %, the full 100 being rarely reached and never more than barely exceeded. A careful investigation of plankton has not been made in Pond Lluest but the writer's impression is that it is scanty; the oxygen variations are probably those to be associated with a pond of the oligotrophic type.

Butcher *et al.* (1937, p. 38) show that diurnal oxygen changes in the upper waters of the river Tees at Eryholme (some sewage pollution being present) ranged from 60 to 163 % saturation during 24 hr. which included a sunny day in summer (3-4 July) in presence of the filamentous alga *Cladophora*. During a similar period, including also a sunny day (7-8 August), but in the absence of *Cladophora* the range was only from 80 to 90 %. The same investigators support by experiment their statement that the water of the upper Tees can become saturated with oxygen only as a result of photosynthesis.

Emerging from the above consideration of the seasonal and diurnal changes in the dissolved oxygen content of rivers and ponds it appears that temperature and air are of much greater importance, and plant activities of much less importance, in both the Afon Tuen and Pond Lluest than in rivers and ponds described by other workers. In the Afon Tuen indeed temperature and air mask any small effects occasional green plants may be having, so that the oxygen curve is highest in the hours of darkness and lowest in the afternoon. Pond Lluest appears to be an example of an oligotrophic pond in contrast to the apparently eutrophic ponds investigated by others.

5. EXPERIMENTS CONCERNING THE EFFECT OF ATMOSPHERIC OXYGEN AND DECOMPOSING ORGANIC MATTER ON THE DISSOLVED OXYGEN IN THE WATER

The curves representing the diurnal oxygen cycle in the pond, considered above, suggest that the main factor determining their form is the effects of green plants, the upward course as light intensity increases being associated with photosynthesis, and the downward course, as darkness grows, with respiration, the absorption of oxygen due to this function becoming obvious with the cessation of photosynthesis. Other factors which help to determine the oxygen content of the water are the absorption of oxygen from the air on the one hand, and, on the other, the loss of oxygen due to decomposition processes. Experiments were made with a view to determining in a general way the respective contributions of these factors.

A. On 10 September a small patch of the pond was cleared of *Equisetum* stems and a galvanized iron frame covering a square 15 × 15 in., having sides 18 in. deep, and open above and below, was placed on the pond bed exposed, thus isolating a volume of water. The top of the frame reached a couple of inches above the water-level. Dissolved oxygen was estimated for the water inside the frame, and also for that of the pond just outside, among the *Equisetum* stems, at about sunrise and at 3 p.m. G.M.T. each day over a period of 6 days. The results are given in Table 9 and Fig. 6, each record being the average of two estimations.

Table 9. *Experiment A. The effect of green plants and of decomposition upon the amount of dissolved oxygen in the water, 10–16 September 1941*

Date (Sept.)...	10	11		12		13		14		15		16	
G.M.T.	... p.m.	3 a.m.	3 p.m.	6 a.m.	3 p.m.								
Dissolved oxygen mg./l.													
<i>Equisetum</i> area outside frame	6.5	4.3	6.8	5.3	8.8	6.5	10.6	7.2	10.0	7.0	9.6	5.6	10.7
Inside frame over mud	5.0	4.6	4.4	4.3	4.1	4.3	4.4	4.3	4.2	4.8	4.3	4.5	4.3
Temp. °C.													
<i>Equisetum</i> area outside frame	15.5	14.8	15.5	14.3	15.0	14.0	15.0	14.0	15.4	13.7	14.6	13.0	15.8
Inside frame over mud	15.5	14.8	15.5	14.0	15.2	13.8	15.5	13.9	15.4	13.5	14.4	12.5	15.5
Dissolved oxygen at saturation mg./l.													
<i>Equisetum</i> area outside frame	10.0	10.1	10.0	10.3	10.1	10.4	10.1	10.4	10.0	10.4	10.3	10.6	9.9
Inside frame over mud	10.0	10.1	10.0	10.4	10.1	10.4	10.0	10.4	10.0	10.5	10.3	10.7	10.0
Dissolved oxygen, percentage of saturation value													
<i>Equisetum</i> area outside frame	65	43	68	51	87	63	105	69	100	67	93	53	108
Inside frame over mud	50	46	44	41	41	41	44	41	42	46	42	42	43

Attention may be called to the following features:

(i) The oxygen for the water outside, among the *Equisetum* stems, shows the expected diurnal cycle, involving alternating afternoon peaks and early morning troughs. The masking of the effects of the temperature factor by this is clearly demonstrated, the general form being inversely related to expectation based on temperatures.

(ii) Since the water inside the frame is cut off from the green plant influence, the curve representing its contained oxygen does not show the characteristic diurnal cycle of the

water of the pond outside. But of perhaps greater interest is the low oxygen content indicated. It was noted that the water in the frame failed to clear, due to the disturbing effect of the latter upon the mud as it swayed gently through the impact of wind and water, and the low oxygen content can be associated with the presence of oxidizable material derived from the muddy bottom. An equilibrium was established, for the duration of the experiment, some 5·5–6 mg./l. below saturation, being a percentage saturation of 41–46. Towards the close of this experiment the pond bed in the surrounding *Equisetum* area was disturbed, so that fine mud clouded the water. A reduction in oxygen took place from 10 mg./l. (saturation 10·2 mg./l.), just before the disturbance, to 8·7 mg./l. estimated half an hour later for water collected 3 min. after the disturbance. The water in the disturbed region very soon completely cleared.\*

B. A galvanized iron bath of 35 l. capacity was nearly filled with water from the pond, to a depth of 25 cm., and sunk into the pond so that the level of the water inside and outside the bath was the same. The surface area of the water in the bath was about 1600 sq. cm. A second bath was similarly filled with water, and a quart of wet mud added. The temperature and oxygen content were recorded for the water of each of the baths, and of the pond in the adjacent *Equisetum* area, at about sunrise and at 2 p.m. G.M.T., for 5½ days. For the later portion of this period the same data were recorded for the stream. The results are shown in Table 10 and Fig. 7. Each record is the average of two estimations.

The following features emerge:

(i) The oxygen curve for the *Equisetum* area is of the same character as in Exp. A above. From a comparison with the oxygen curve of the clear water it appears that the net effect of plant activities is, for the greater part of the 24 hr., to reduce the amount of oxygen below what it would have been in their absence.

(ii) In the bath to which the mud was added, the initial effect was to reduce the oxygen markedly, to an extent similar to that in Exp. A. But the bath was steady as compared with the frame, so that the mud settled in it much more rapidly than in the latter. The oxygen dissolved from the air was thus used up to a much lesser degree, the form of the curve suggesting however that an equilibrium would have been established before reaching the values for clear water. The experiment terminated at this point owing to a very heavy rainfall raising the level of the pond above that of the baths. Previously there had been no rain during the experiment.

As a continuation experiment the bath was raised and the mud stirred. A sample was taken after 5 min., an oxygen estimation for which, half an hour later, showed a drop in oxygen from 10 to 6 mg./l. (saturation 10·7); 2 days later it had risen to 8·2 as

\* In order to be sure that there was no direct reaction between the mud and the iodine solution used in the Winkler determination, the following experiment was performed:

A dilute solution of iodine in potassium iodide was titrated in the usual way, with N/56 hypo solution. Two determinations gave the following readings:

1·50 c.c. iodine solution	7·0 c.c. N/56 hypo.
2·50 c.c. " "	7·1 c.c. "

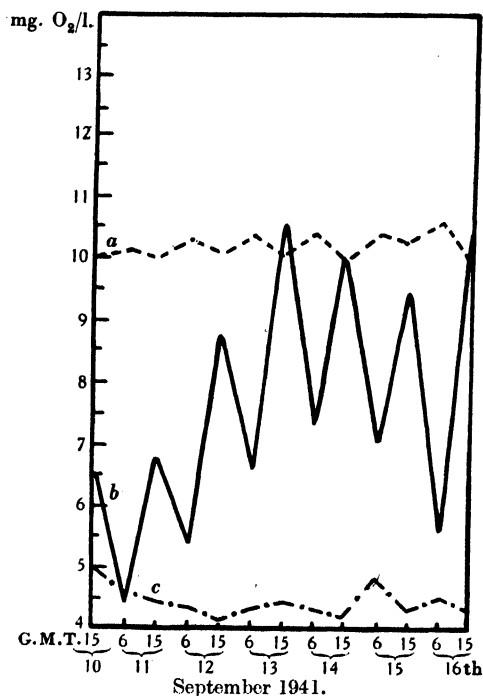
Samples of suspensions of the mud were added to 50 c.c. volumes of the same iodine solution, allowed to stand 3–4 min., and the mixtures titrated with hypo solution:

1·50 c.c. iodine solution plus mud	7·2 c.c. N/56 hypo.
2·50 c.c. " "	7·05 c.c. "

From these results it can be concluded that as long as the suspension of mud is not so thick as to make determination of the end point of the titration impossible, no appreciable error is introduced.

Table 10. *Experiment B. The effect of green plants, of air, and of decomposition upon the amount of dissolved oxygen in the water, 11–16 October 1941*

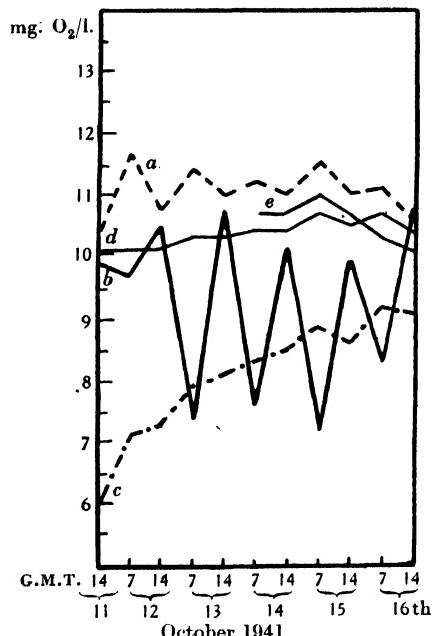
Date (Oct.)	11	12		13		14		15		16	
G.M.T. ...	... 2 p.m.	7 a.m.	2 p.m.								
Dissolved oxygen mg./l.											
Equisetum area	9.9	9.7	10.5	7.3	10.8	7.5	10.1	7.1	10.0	8.2	10.7
Isolated water	10.1	10.1	10.1	10.3	10.3	10.4	10.4	10.7	10.5	10.7	10.4
Water over mud	6.0	7.1	7.3	7.9	8.1	8.3	8.5	8.9	8.6	9.2	9.1
Stream	—	—	—	—	—	10.7	10.7	11.0	10.7	10.3	10.1
Temp. °C.											
Equisetum area	14.5	10.5	12.7	10.4	11.1	10.9	11.1	10.1	11.1	11.1	13.0
Isolated water	14.1	8.8	12.5	9.7	11.2	10.6	11.2	9.5	11.2	11.0	12.8
Water over mud	14.1	9.2	12.3	9.5	11.8	10.5	11.2	9.3	11.2	11.0	13.0
Stream	—	—	—	—	—	10.9	11.5	9.9	11.2	11.0	12.0
Dissolved oxygen at saturation mg./l.											
Equisetum area	10.3	11.2	10.7	11.2	11.1	11.1	11.1	11.3	11.1	11.1	10.6
Isolated water	10.4	11.7	10.7	11.4	11.0	11.2	11.0	11.5	11.0	11.1	10.6
Water over mud	10.4	11.6	10.7	11.5	11.0	11.2	11.0	11.5	11.0	11.1	10.6
Stream	—	—	—	—	—	11.1	10.9	11.3	11.0	11.1	10.8
Dissolved oxygen, percentage of saturation value											
Equisetum area	96	87	98	65	97	68	91	63	90	74	101
Isolated water	97	86	94	90	94	93	95	93	95	96	98
Water over mud	58	61	68	68	74	74	77	77	78	83	86
Stream	—	—	—	—	—	96	98	97	97	93	94



The curves represent dissolved oxygen:

- a, at saturation (among *Equisetum* stems);
- b, in pond among *Equisetum* stems;
- c, in pond water over mud, isolated in bath;
- d, in pond water isolated in bath;
- e, in the stream.

Fig. 6. Exp. A, on the effect of green plants and of decomposition upon the amount of dissolved oxygen in the water.



The curves represent dissolved oxygen:

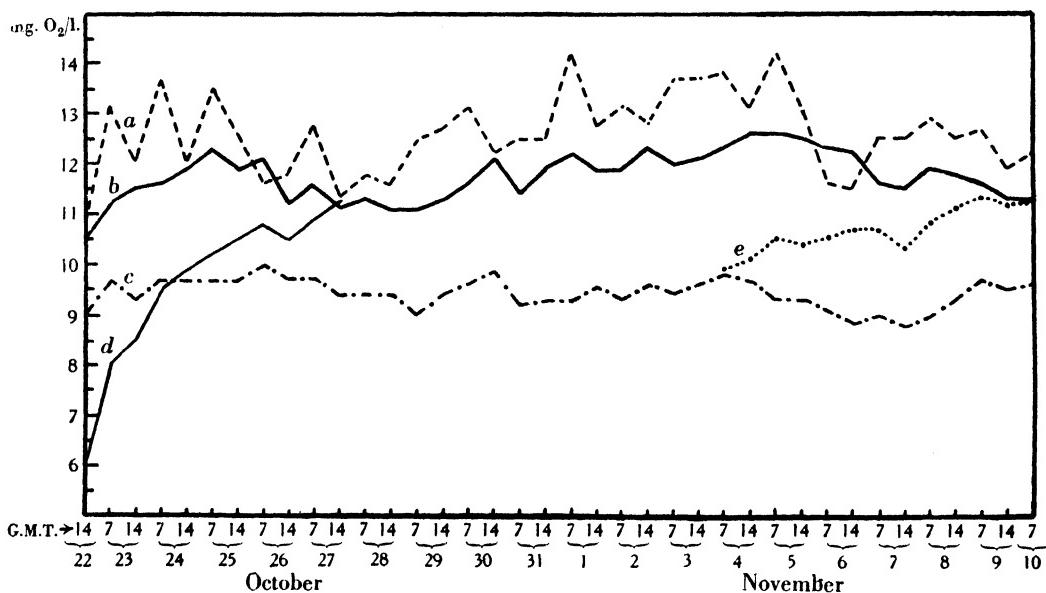
- a, at saturation (among *Equisetum* stems);
- b, in pond among *Equisetum* stems;
- c, in pond water over mud, isolated in bath;
- d, in pond water isolated in bath;
- e, in the stream.

Fig. 7. Exp. B, on the effect of green plants, of air, and of decomposition, upon the amount of dissolved oxygen in the water.

against 10.7 in the open pond (saturation 10.7); and a week later it was 10.3 as against 11.1 in the open pond (saturation 11.8).

(iii) The bath of clear water isolated from both plant influence and the influence of decomposing matter shows oxygen content not far short of saturation, with a tendency more marked during the last 2 days, to move inversely in relation to the curve due to plant influence, as though determined by temperature as in the case of the water of the stream.

C. Three galvanized iron baths, as in Exp. B, were placed in the open air in a garden in Aberystwyth. One was nearly filled (to within 2 in. of the top) with tap water which had been shaken so as to increase its oxygen content. In a second was put the same amount of tap water, which had been heated to remove some of the dissolved oxygen.



The curves represent dissolved oxygen:

*a*, at saturation, in tap water;      *b*, in tap water;      *c*, in tap water over mud from pond;  
*d*, in tap water with oxygen reduced;    *e*, in water removed from *c*.

Fig. 8. Expt. C, on the effect of air and of decomposition upon the amount of dissolved oxygen in the water.

In the third was put tap water having the same oxygen content as the first, and to this was added a quart of wet mud from the pond. The oxygen content was estimated in each of the three baths at about sunrise and 2 p.m. G.M.T. each day over a period of 11 days. The weather was in the main fine during the experiment. On one occasion only was there substantial rain, during which the baths were temporarily covered. The results are shown in Fig. 8.

The following features will be observed:

(i) In the bath containing the mud, the latter was allowed to settle for an hour before the oxygen was estimated. A reduction of 2 mg./l. as compared with the amount of dissolved oxygen in the water in the first bath was then recorded, the values remaining at approximately this level throughout the 18½ days of the experiment, and the water

clear. At a date later than those included in the graph the water was stirred, with the result that there was an immediate drop of 2 mg./l. in the oxygen content. On 4 November a portion of the water was removed to a separate vessel. In the absence of the muddy sediment at the bottom the oxygen content of this water gradually increased, until in 6 days it had reached that of the clear water. Sustained reduction of oxygen therefore depends upon a continual renewal of oxidizable material from the mud.

(ii) As in Exp. B above, the bath which commenced with water of high oxygen content retained an oxygen content little below saturation throughout the period. The tendency to a time lag in relation to temperature will be noted.

(iii) The oxygen curve for the clear water in which the oxygen had been reduced to 6 mg./l. by heat, gives some idea of the rate of absorption of oxygen from the air. It was restored to 11 mg./l., the value for the unreduced clear water and approximate saturation, in 5 days.

D. From the above experiments it is clear that the presence of mud in the water reduces the amount of dissolved oxygen therein. It was thought desirable to make some analysis of the materials in the mud responsible for reducing the oxygen. To this end estimations were made by the Forchammer Process, as follows, the results being expressed as grams per 100,000 c.c.:

Oxygen consumed by	...	(a)	(b)	(c)
		15 min. at 27°C.	Subtract (a) from (c)	4 hr. at 27°C.
		Nitrites, ferrous salts, and H <sub>2</sub> S	Organic matter	Total
(i) 15 Nov. Aberystwyth tap water		0.079	0.032	0.111
(ii) 8 Nov. Open water from Pond Lluest		0.106	0.067	0.173
(iii) 13 Nov. Water from Pond Lluest immediately after disturbance of muddy bed		0.269	0.235	0.504
(iv) 13 Nov. Water from bath after stirring up of Pond Lluest mud which had been lying in it undisturbed for some weeks	0.330	0.203	0.533	

The mud disturbed in (iii), which was in the *Equisetum* area, was odorous, and doubtless the considerable increase under the first column is due in large measure to H<sub>2</sub>S. The mud in (iv) was brought from the same region.

It may be concluded from the above observations and experiments that the main factor in determining the form of the diurnal oxygen curve is the activity of green plants; that without green plants and without decomposition the influence of the air alone is sufficient to maintain a persistently high oxygen content, only slightly below saturation; that the mud contains substances capable of rapidly absorbing oxygen from the water, but that these are ordinarily diffused into the water in quantity not greater than can be counteracted by the oxygen from the air, or than can be removed by water movement (in which connexion the through-flowing stream must be borne in mind); that the oxygen from the air is not only sufficient to deal with decomposing matter emanating from the mud which may not be carried away by water movement, but also to supplement the oxygen of photosynthesis in mitigating the absorption effects of respiration; that the air has a more important role to play than the *Equisetum* in oxygenating the water; and that the net effect of *Equisetum* metabolism is to reduce oxygen content.

In association with the above experiments, and indeed with the observations upon the pond generally, the question of oxygen gradients arises. Air and mud might be thought

to co-operate to produce a gradient showing a diminution of oxygen from above downwards, and it might be suggested that there should be others, related to the respiratory and photosynthetic activities of green plants.

It was outside the scope of the present study to attempt to trace any gradients that might be present, other than to make a very general sampling prior to deciding at what level to take the water samples for the routine estimations. The method was to lower carefully a bottle to different depths by hand. From estimation of the dissolved oxygen in such samples it appeared that there was no material difference in amount of dissolved oxygen from the surface to within a couple of inches of the bottom. The lowest 2 in. or so could not be satisfactorily sampled by the technique adopted, since a disturbance of the mud was caused, and introduction of mud into the sample results in using up of oxygen.

The following are some results obtained, oxygen being expressed as mg./l.:

21 October. 3.45 p.m. in water 2 ft. deep in *Equisetum* area. Surface 10.93; at 1 ft. depth 10.73.

8 November. 3 p.m. in water 1½ ft. deep in *Scirpus* area. At 1 ft. depth 11.54; 3 in. from bottom 11.69.

12 November. 1.30 p.m. in water 15 in. deep in *Equisetum* area. Surface 9.78; 4 in. from bottom 9.28.

12 November. 4.40 p.m. in clear water 15 in. deep, above mud, free from vegetation. Surface 10.73; 4 in. deep 10.90 and 11.05; 8 in. deep 10.93; 1 ft. deep 10.83.

Such differences are in nearly all cases within the experimental error.

Adeney (1926) described laboratory experiments on columns of quiescent deaerated water, 3, 6 and 10 ft. in depth, exposed to air. He states that 'the columns became aerated gradually, and more or less uniformly, from top to bottom during every step of the process of aeration, until completely aerated'. This he explains by evaporation leading to cooling of the surface layer, which then sinks downwards. Adeney's experiments appear of interest in the present connexion, though the conditions under which they were made differ from those at the pond in that the surrounding temperature was uniform, and there could be no lateral movement of the water such as is associated with the through-flowing current. It seems probable that any oxygen gradients in Pond Lluest would be of a very partial and transient character, disturbed by changing water temperatures, vertical streaming and lateral movement. It may be remarked that on a hot day the mercury in a thermometer is readily seen to fall as the thermometer passes from the surface layer to water below, and at a temperature below 4° C. the reverse is seen.

#### 6. COMPARISONS BETWEEN THE DIFFERENT POND STATIONS

The pond stations fall into two groups; one includes the two regions of richest vegetation, namely, *Equisetum* and *Potamogeton*, and the other consists of the two stations most free from vegetation, namely, the open water near the outlet, and the *Sparganium*. The relative data are included in Table 1.

Observations were made in regard to wind, rain, water-level, and hours of sunshine, as well as temperature. Except in the case of hours of sunshine, an attempt to explain differences between the various curves on the same date by reference to these records did not lead to any clear results. No doubt the influences named act differentially upon

different regions of the pond, but the results are obscured by the interacting of a variety of factors, the equalizing action of water movements, and, of considerable significance, the fact that the dissolved oxygen is ordinarily very close to saturation. An analysis of windy and calm days shows that on the former the open water has actually in the majority of cases a higher oxygen content in relation to the water of the *Equisetum* station, but, knowing other factors to be involved, it would be extremely rash to suggest that in all, or even in any, of the cases, the wind is the critical factor. Or to compare two windy days: on 5 December, with a strong south-west wind and a little rain, the oxygen was high in the open water, but on 23 October, with an equally strong wind though on this occasion dry, north-east, it was relatively low; in the absence of other factors the reverse would have been expected.

But one factor appears significant as a differentiating agent, namely, sunshine. During seasons of active plant metabolism, dull days would be expected to differentiate oxygen content, as between *Equisetum* and open water areas, in favour of the latter, and days of very bright sun in favour of the former. On ten occasions between the commencement of April and the end of October the hours of sunshine did not exceed two; of these, seven (31 October 1940, 9 April, 23 May, 9 June, 13 July, 2 September, and 9 September 1941) correspond with expectation, but three (3 April, 16 September, and 7 October) do not. Similarly on the very sunny days, there are 8 days during the period named, on which the hours of sunshine exceed ten; on six of these (17 August, 25 September, 15 May, 20 June, 13 August, and 23 September) the *Equisetum* station is high in oxygen in relation to the open-water one, against two (11 September and 2 August) where anticipation is not realized. The data therefore suggest that sunshine has a differentiating influence, but that other factors are also concerned. Of these, wind is perhaps the most generally important.

It may be noted that there is a general tendency, particularly during the second half of the year, for the 'rich vegetation' stations to indicate less oxygen than the open 'open water' ones. This tendency is more marked in the *Equisetum* stations than in those for *Potamogeton*. That is to say, even at the period of oxygen maxima the water of the main vegetation zones is, on the average, less highly oxygenated than the open water. Regarding the tendency of the *Equisetum* stations to be lower in oxygen than those for the *Potamogeton*, insufficient is known about the physiology of the two plants to enable the difference to be referred thereto. It may with greater probability be referred to differences in the amount of decomposing organic matter in the bottom deposits of the two stations. No actual analyses have been made, but it seems evident from a general inspection that decomposing material is in considerably greater abundance at the *Equisetum* station, and the natural suggestion would appear to be that the dramatic drop in the *Equisetum* oxygen curve in August 1940, and again in December 1940, and in September 1941, are associated with decomposition of organic matter.

## 7. SUMMARY

1. This paper is concerned with the changes in the amount of dissolved oxygen in the water of a pond, and its inflowing stream, situated at an altitude of about 1000 ft. above sea-level.
2. Approximately weekly estimations of oxygen were made from the beginning of August 1940 to the end of October 1941, and records of temperature from the end of

September 1940 to the end of October 1941. Five (sometimes six) stations were sampled in the pond, and one in the stream, on each occasion.

3. In the stream, which is almost entirely free from vegetation, oxygen concentration changes, both diurnal and seasonal, are essentially determined by temperature changes. The diurnal oxygen curve is highest in the night and lowest in the afternoon. This is in contrast to vegetation-containing streams and rivers investigated by other workers.

4. In the pond, which contains vegetation, oxygen concentration is essentially determined by temperature and the photosynthetic and respiratory activities of living organisms. The oxygen concentration maxima attained during the hours of sunlight have a seasonal variation corresponding to seasonal temperature changes, but during the hours of darkness, in the absence of photosynthesis, the effect of the consumption of oxygen by respiration becomes evident, leading to a reduction in oxygen concentration which renders this relationship much less close. The diurnal cycle has, during the season of plant activity, an afternoon peak and an early morning trough.

5. The seasonal dissolved oxygen percentage saturation curves indicate, for both pond (diurnal maxima) and stream, a saturation of rather less than 100% ordinarily, the full 100 being rarely reached and barely exceeded. The association of hours of sunshine with the increased fluctuation of the pond curve during the months of activity of the larger plants is very noticeable.

6. Experimental evidence is given regarding the effect of atmospheric oxygen and decomposing organic matter respectively, on the amount of dissolved oxygen. It is concluded that in this pond, which would appear to be of the oligotrophic type, the former is by far the more important, effectively neutralizing the latter, but that neither masks the effect of plant physiology on the general form of the diurnal oxygen curve. It is further concluded that the net effect of both *Equisetum* and *Potamogeton* physiology is to reduce the dissolved oxygen to below the level at which it stands in their absence; the oxygen content in these vegetation regions barely reaches that of the open water even at the period of the diurnal maximum.

7. The differences between the records for the five pond stations on the same date, taken during the hours of maximum oxygen content, are not ordinarily great, nor do they show much consistency, save that there is a recurrent tendency for the 'vegetation' curves to show lower oxygen values than those for water free from plants. Possible factors responsible for differences are reviewed, but no clear conclusions emerge save that there are indications of the differentiating action of light intensity, acting through plant activity.

The writer expresses her grateful thanks to the following: Dr J. R. E. Jones, for suggesting the topic of this investigation; Prof. R. D. Laurie and Dr J. R. E. Jones for helpful advice during its progress; Prof. T. A. Stephenson for kindly reading through the manuscript; Mr E. H. Chater, and to Mr E. G. Bowen and Captain David Jones for help in reference to sun-record data and calculations. The writer also thanks the Ystumtuen Anglers' Association for permission to investigate the pond.

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A paper by Whitney (1942) has been published while this has been in the press. In it are recorded certain diurnal changes in the oxygen content of two small lowland ponds and a stream. The pond data are consistent with those of Beattie (1930) for the apparent eutrophic Farnham Royal ponds and are in similar contrast with those for Pond Lluest. Winter data for the stream are in agreement with those for December for the Afon Tuern in showing no evidence of a diurnal periodicity at a time when day and night temperatures show little difference.

## R E V I E W S

## THE JOURNAL OF ANIMAL ECOLOGY

VOL. 11, NO. 1, MAY 1942

This number contains eight original papers, two reviews and 140 'Notices of Publications on the Animal Ecology of the British Isles'. D. F. W. Baden-Powell describes how the lack of lime in the sand dunes of Studland Peninsula, Dorset (the site of an important co-operative ecological survey organized by C. Diver), can be explained by the absence of strong wave action for breaking up marine mollusc shells on the shore, these being the chief normal source of lime in dunes. There is a list of the molluscs washed ashore. David Lack contributes an elaborate analysis of the accumulated records of birds on various small islands round the British Isles, and is able to bring out the great variation in these bird faunas, not only from one island or island group to another, but over periods of years. Some instances of marked habitat changes are also mentioned. M. K. Colquhoun gives a note on the numbers of American grey squirrels recorded during walking transects in Savernake Forest, and compares these with similar counts of birds. A strong preference of squirrels for beech trees was indicated. D. W. Williams has verified the life history of the sheep lungworm (*Muellerius capillaris*) through various snails and slugs in South Wales, and the frequency of natural infections in these molluscs. H. F. Barnes describes fluctuations in sample populations of the carrot-fly (*Psila roseae*) and its parasites. The dates of emergence are important in forecasting outbreaks. It was found that watering the base of the carrot clamps with formalin just before emergence of the flies is a good means of control. Another agricultural economic problem is the infestation of cornstacks with rats and mice: the first thorough ecological investigation of these rodent populations, their numbers, seasonal occurrence, breeding rates, and methods of control, is described by L. S. V. Venables and P. H. Leslie. 518 corn ricks were examined and fairly complete populations analysed: e.g. in April 1940 there were on the average 79 rats per rick in the Oxford district.

Charles Elton and Mary Nicholson have assembled the statistical data from fur records and enquiries at posts of the Hudson's Bay Company, about fluctuations in numbers of the Canadian muskrat, and conclude that it has a periodicity similar in length to that of the lynx and snowshoe rabbit (about 10 years). Walter Pickles writes a brief note on the animals he had found killed by traffic on a stretch of road in Yorkshire.

The reviews deal with the *Journal of Ecology*, and with the ecology of the coyote in Yellowstone National Park, U.S.A. The number of Notices again bears witness to the resilience of British natural history and ecology even under wartime conditions. It might be noted that practically all the contributors of original papers in this issue are either in war service or carrying out special wartime research.

CHARLES ELTON.

**Karl H. W. Klages.** *Ecological Crop Geography.* 615 pp., 108 text-figs. New York: The Macmillan Company. \$ 4.50.

This book deals with a somewhat neglected field, the bearing of ecological and other factors on crop distribution. It embodies the results of work on crop ecology as such, although ecological crop geography is considered to include not only these results, but also the economic, historical and social factors which modify them in determining the broad distribution of crop plants. This width of outlook is somewhat disadvantageous since we require to know much more of crop ecology before the wider field can be tackled adequately. Nevertheless, there is no doubt that the attempted integration is valuable and that this work will serve a useful purpose.

After defining the chosen field, the author proceeds to discuss the nature of the environmental factors which may control crop distribution. These fall mainly into two groups, those dealing with physiological effects and those which are social and economic in character. The treatment accorded to the physiological effects of the environment is, on the whole, good. It is most fully concerned with the effects of water and temperature, though light and soil effects are not neglected, nor such subjects as drought and frost resistance. It leads on to the attempt to evaluate climatic indices of plant distribution along the lines

made familiar by the work of Koppen and Thornthwaite and finally to the discussion of the distribution of important crop plants.

Considerable importance is attached to one ecological generalization. It is shown from the study of crop yields and their annual variation that the optimum ecological conditions for a given species are not only marked by the largest average yields but also by least variation in yield from year to year. The data are based mainly on the relation of cereal crops to rainfall and hence refer to seed production, but no doubt the generalization could be applied to other conditions, for the annual variations of species at the limits of their ecological and geographical ranges are often very marked.

The general impression left on the reviewer's mind is that this is a courageous attempt at integration in a wide field. It is informative and well supplied with references and maps, and it is certainly a useful work of reference. There are undoubtedly considerable gaps in the integration, probably inherent in the material available, and these should serve to promote further investigation. They are evident, perhaps most clearly, in the treatment of the effects of light intensity and duration as environmental factors, a field in which little geographical work has been done. One would also like to see a somewhat fuller discussion of the question how far the available climatic indices are really useful in the delimitation of the ranges of vegetation types. This would no doubt necessitate a detailed consideration of some selected area. One gets a general impression that the geographical method of attack, based largely on apparent correlation in distribution, and the physiological and ecological methods, have by no means succeeded in meeting.

Enough has been said in this brief review to show that the book usefully summarizes much important work and presents an instructive point of view. It should therefore find a place on most ecological book-shelves.

W. H. P.

**BIOLOGICAL FLORA OF THE BRITISH ISLES**

L.C. (Ed. 11) No. 902

**Aster Tripolium L.**

BY A. R. CLAPHAM, W. H. PEARSALL AND P. W. RICHARDS

MAINLY FROM DATA PROVIDED BY V. J. CHAPMAN

Sect. TRIPOLII Nees. Stem 1–2 ft. (30–60 cm.), erect, glabrous, leafy, branched. Leaves alternate, fleshy, three-nerved, entire or faintly denticulate. Radical and lower cauline

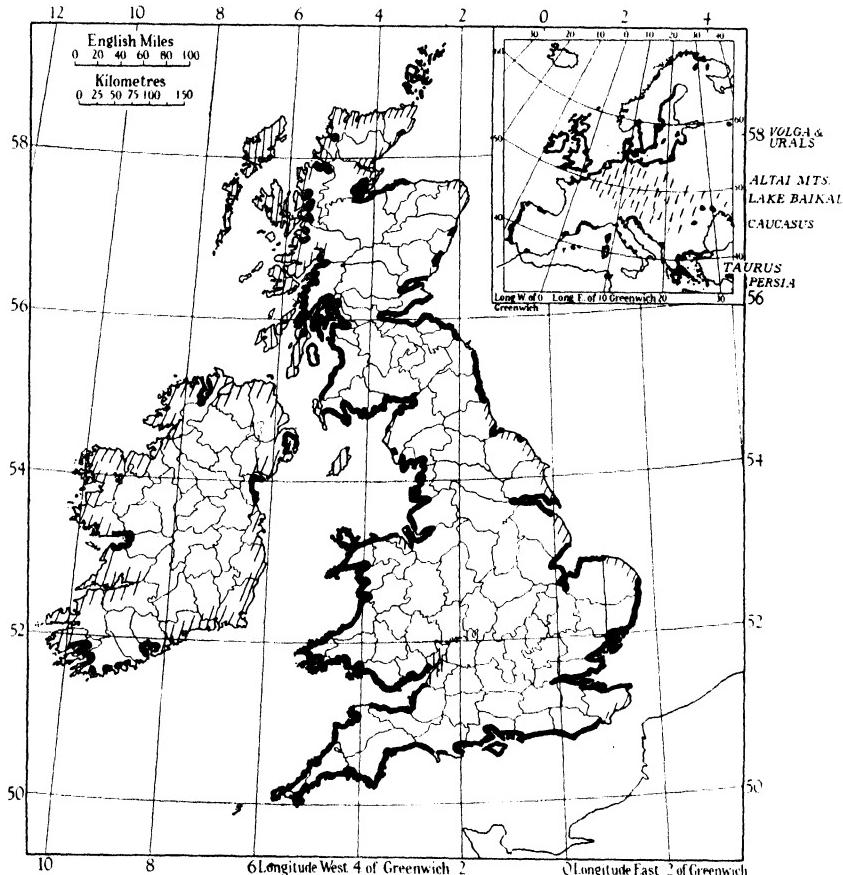


Fig. 1. Distribution of *Aster tripolium*. Light shading represents via countries from which it is reported but with no indication of locality. Full black represents areas in which Dr Chapman or other observers have seen the plant growing.

leaves oblanceolate or obovate; upper leaves linear-lanceolate. Heads in a corymb, numerous (25–100),  $\frac{1}{2}$ – $\frac{3}{4}$  in. (0.8–1.6 cm.) diam. Involucral bracts imbricate, the inner longer, all appressed and scarious-tipped. Disk florets yellow, ray florets bright blue to lilac, occasionally white, often absent (var. *discoideus* Reichb.). Fruit hairy. Pappus dirty white.

Besides var. *discoideus* Reichb. several other varieties (see under I below) have been reported from Britain, but their taxonomic status is not known.

A common salt-marsh plant of the seashore and to the tidal limit in estuaries: occurring also on cliffs and rocks near the sea, and in inland saline areas.

I. *Geographical and altitudinal distribution.* Recorded from all British and Irish vice-counties bordering the sea, except Banff (94), and ascending the Severn estuary to east and west Gloucestershire (34, 35). It is locally abundant in suitable habitats south of a line drawn from the Humber to the Cheshire Dee, but farther north it is almost confined to estuaries. It is abundant along the Forth and Tay, rare near Aberdeen, and on the

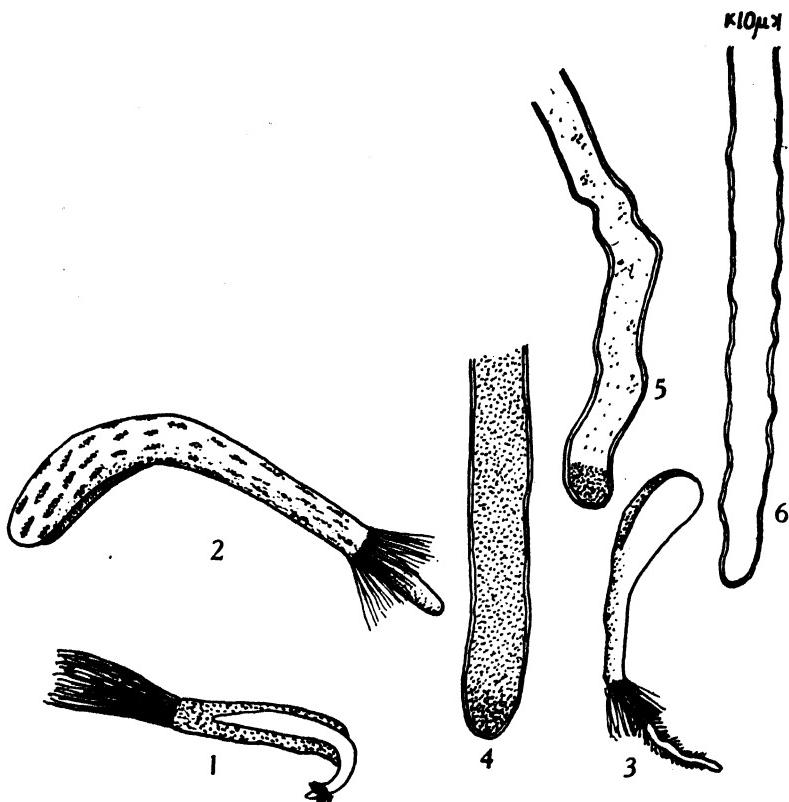


Fig. 2. 1, Germinating seed.  $\times 3$ . 2, 2-day old seedling.  $\times 5$ . 3, 5-day old seedling.  $\times 3$ . 4–6, increasing age stages in rhizoidal hairs.

west coast of Scotland is confined to marshes at the heads of the lochs and to suitable areas along the Clyde. In Ireland it is found all round the coast in salt marshes and estuaries and also on rocks.

It is found inland at the Cerebos saltworks at Greatham, Co. Durham, where the brine overflow raises the salinity to 4·6% (Chater). It is also said to occur in Staffordshire (Richards).

Frequent on most of the European sea-coast including the west shore of the Baltic and the east shore as far north as the Gulf of Riga, but absent from Iceland and the Faeroës. Very local in Norway but recorded from Varanger Fjord (c. 70° N.), and from Lakes Enara, Imandra, etc., in Lapland. Occurs on the shores of the Mediterranean, including

Tunis; and of the Black Sea, the Caspian Sea and Lake Baikal. Also recorded from inland saline areas in central Europe and Asia, including the Taurus.

Var. *discoideus* Reichb., with no ray florets, has been recorded from many English and Welsh localities south of a line between the Isle of Man and Whitby, Yorkshire, and from

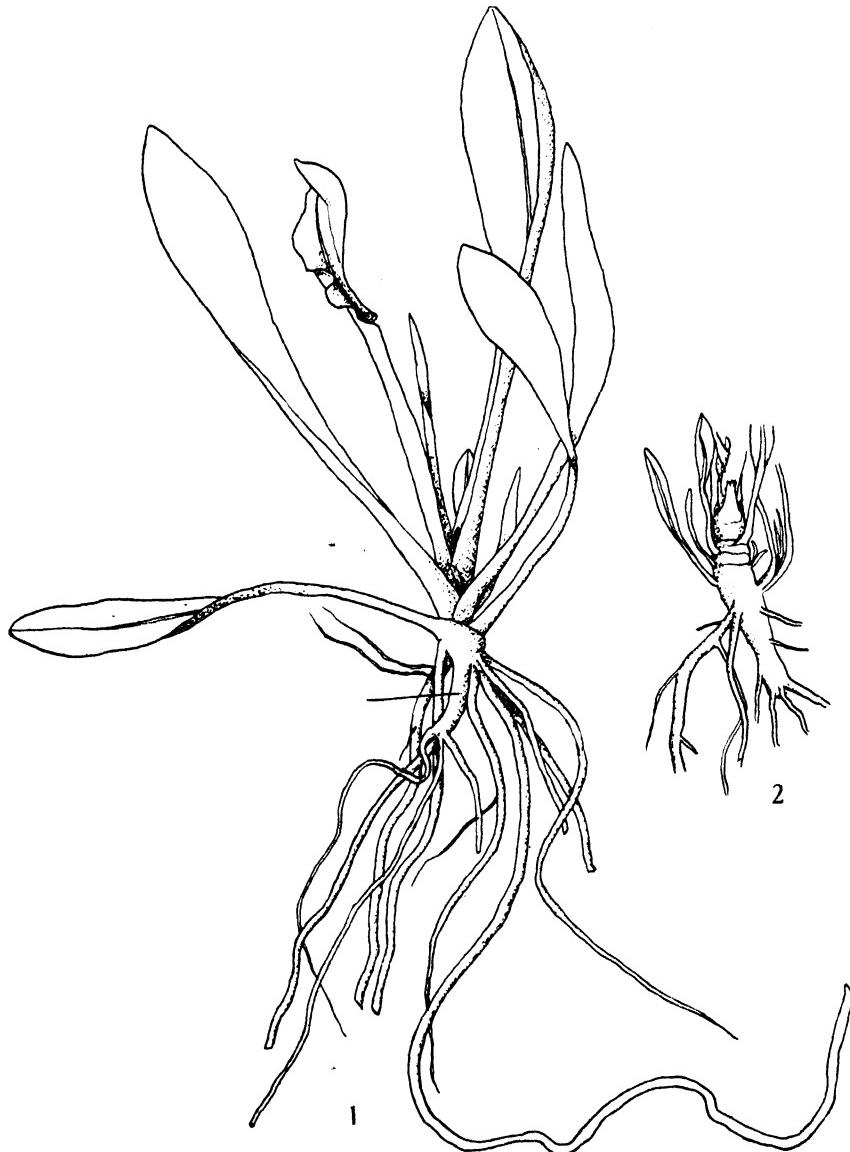


Fig. 3. 1, 18 week plant.  $\times 1$ . 2, 8 month plant, basal portion.  $\times \frac{1}{2}$ .

two isolated Scottish localities, viz. Leith (Midlothian, 83) and Garlieston (Wigtown, 74). There is one German record.

Var. *arcticus* Fries, a dwarf form with basal branching, is recorded from north Scotland (Hebrides and Orkneys), Norway (Varanger Fjord) and Sweden.

\*Var. *crassus* V. J. Chapman, short and stout with larger leaves than in the type, has been recorded from cliffs in Pembroke, Cornwall and the Orkneys.

Vars. *glaber* Bolzon and *longicaulis* (Duf.) Rouy have also been reported from Britain. Some or all of these varieties may be non-heritable phenotypic forms (ecads).

Chiefly found between 0 and 25 ft. (0 and 8 m.) above sea-level, but var. *crassus* V. J. Chapman grows at higher levels on cliffs. Some inland localities in central Europe and Asia are about 1300 ft. (400 m.) above sea-level.

II. (1) *Habitat.* Generally in salt marshes with frequent tidal inundations, and confined naturally to saline habitats, but can be grown in non-saline soils and shows optimal development in slightly brackish conditions. Found over a wide range of soils and climates. Where the soil is sandy and drains easily it occurs only on the lower marshes, but reaches higher levels on soils of finer texture. This may be related to its intolerance of very high salinities (see under II (2) (j) below).

Table 2a. *Tidal relations of Aster Tripolium*

Locality	Level (o.d.) ft.	No. of submergences per annum
Upper limit	+ 9.79	166
Upper limit of abundance	+ 9.02	234
Near upper limit of dominance	+ 8.23	344
Near lower limit of dominance	+ 8.09	362
Lower limit	+ 6.45	567

(Mean height of neap tides in 1933 = + 5.30 ft. o.d. Mean height of spring tides in 1933 = + 10.28 ft. o.d.)

Table 2b. *Tidal relations of Aster Tripolium*

Locality (see Table 2a)	Periods of greatest submergence	Max. non-tidal exposure days	Month of max. non-tidal exposure	Average hours sub- mergence per month		
				Total	In daylight	
1	Mar., Oct.	25	June-July	10.5	0.35	
2	Mar.-Apr., Oct.-Nov.	22	June-July	30.1	0.70	
3	Jan., Mar.-Apr., Aug.-Oct.	22	June-July	57.5	1.20	
4	Oct.	10	Jan., May-June	70.0	1.20	
5	Jan., May, July, Nov., Dec.	5	Feb., Mar., Apr., May, Sept.	148.0	2.70	

(2) *Substratum. (a) (b) Parent material and soil profile.* Grows on all salt-marsh soils of British coasts, ranging from sands to clays, and including the peaty silts which seem characteristic of the south-west Irish marshes.

(c) *Tidal relations and water table.* On the Norfolk marshes *Aster* is abundant between + 6.45 ft. o.d. and + 9.04 ft. o.d., but it will extend up to + 9.8 ft. o.d. It grows, therefore, on both upper and lower marshes (Chapman, 1938). Its tidal relations are shown in Tables 2a and 2b. The periods of non-tidal exposure are probably critical on the upper marshes and play a considerable part in restricting the species to communities in which the other vegetation (e.g. *Juncus maritimus*) reduces the loss of water by evaporation. Where drainage is good one-year-old plants wilt after a day's exposure to sun (Montfort & Brandrup, 1927).

The water-table in Norfolk marshes where *Aster* grows shows cyclic changes in level which are determined by the tidal cycle of 14–15 days. Only within short distances of creeks can a daily periodicity in level also be detected. During spring tides the water-table rises slowly, reaching its maximum height a day or two after the highest spring tide.

\* It is proposed to publish a detailed description of this variety subsequently.

On salt marshes with a firm and fine-grained substratum a gas-containing layer is trapped between the subterranean water-table and the surface water during a flooding tide. Analyses at four sites showed that this contained on the average 3.25% CO<sub>2</sub> and 1.16% O<sub>2</sub>. Most of the roots of *Aster* are in this layer.

*Accretion.* Table 3 summarizes data on the rate of accretion in marshes where *Aster* grows.

Table 3

Locality	Authority	No. of sites averaged	Average rate of accretion mm. per annum
Denmark	Neilson (1935)	13	3.6
Dovey Estuary	Richards (1934)	9	3.4
Norfolk	Steers (1939)	34	9.0

On the basis of these data it can be calculated that the early *Aster* stage (vertical range +7.4 to +8.3 ft. o.d.) lasts for about 28 years, and on the Norfolk marshes the succeeding Late Asteretum (vertical range +8.3 to 8.9 ft. o.d.) for about 20 years.

(d) No information.

(e) *Rate of decay of humus.* Variable. Usually rapid, but in south-west Ireland silty peat-like humus is formed. Old dead roots do not disappear very rapidly in the mud of the Norfolk marshes and their cavities form local gas-pockets.

(f) *Appearance of 'peat'* (in south-west Ireland). Fibrous plant remains, chiefly matted roots, with much silt. Unstratified.

(g) *pH.* In salt marshes with *Aster* the pH of the substratum is maintained by tidal water at 7.2-8.2 (Chapman, 1938; Morss, 1927; colorimetric determinations).

(h) *Humus content.* See Table 4.

(i) *CaCO<sub>3</sub> content.* See Table 4.

(k) *Mechanical analysis.* See Table 4.

Table 4. Composition of typical soils on which *Aster* occurs

Locality	<i>Aster</i> frequency	Percentage of air-dry weight					Community
		Humus	CaCO <sub>3</sub>	Sand	Clay	Silt	
Montrose	a.	20.1	—	7.9	23.4	37.7	Glycerietum
Tayport	+	4.5	—	57.4	6.4	22.5	—
Eden	a.	14.5	0.2	11.1	23.9	36.1	Glycerietum
Northfleet	c.d.	17.9	8.0	4.4	39.5	15.5	Glycerio-Asteretum
Cardiff	c.d.	13.5	7.8	1.7	41.5	25.7	—
Tollesbury (a)	+	18.2	0.9	4.8	37.9	17.4	—
Tollesbury (b)	+	13.6	0.1	10.9	37.8	21.1	—
Shoreham	+	4.3	17.6	46.3	13.2	11.5	—
Sunk Island (a)	c.d.	7.0	14.1	13.5	26.1	34.0	Glycerio-Asteretum
Sunk Island (b)	o.	11.8	8.2	1.2	47.0	22.1	G.S.M.
Beal	+	3.7	1.9	84.3	1.1	6.4	—
Norfolk, surface	d.	13.6	3.4	9.6	33.9	31.5	Asteretum
Norfolk, 1 ft.	d.	2.7	2.1	75.6	8.7	7.1	—
Lincolnshire (a)	s.d.	11.7	11.0	20.8	20.6	25.9	Festucetum
Lincolnshire (b)	s.d.	9.5	2.7	38.1	13.5	31.9	—
Dovey: Surface	o.	9.5	—	14.1	48.7	23.9	Armerietum
Subsoil	o.	8.4	—	10.6	44.9	21.9	—
Dovey: Surface	o.	5.5	—	67.7	24.2	0.9	Lower Festucetum
Subsoil	o.	4.8	—	72.4	21.7	0.5	—

(j) *Exchangeable bases.* Data from the Norfolk marshes (Chapman, 1939) showed that exchangeable calcium, expressed as parts CaO per 100 parts of water at the time of sampling, was minimal at 3 in. (7.5 cm.) below the surface (1-4%) and increased to 2-7% at 9 in. (22.5 cm.). The surface showed wide variation from 2 to 10%. These figures were higher than for any other community except the Salicornietum. The high surface

values are perhaps relatable to the abundant shells of the mollusc *Sabaneja ulvae* (Pennant) Sowerby. The gradient of increasing CaO from 3 in. downwards may be due to leaching.

Total chloride, expressed as a percentage of water content at the time of sampling, showed, in the same marshes, the following average values, figures in brackets being summer maxima:

Community	Surface	3 in. (7.5 cm.)	9 in. (22.5 cm.)
Salicornietum	2.0 (4)	2.0	1.75
Asteretum	2.0 (4)	2.25	2.0
General Salt Marsh	1.8 (6)	1.8	1.5
Juncetum	1.25	1.3	0.8

Total chloride showed an annual drift of surface values to a minimum in January and February. It fell temporarily after rain and rose to values much above the average during dry periods in summer. This was much less marked in marshes with *Aster* dominant or abundant than at higher levels. Montfort & Brandrup (1927) concluded that the optimal chloride content for *Aster* lay between 0.0 and 0.39% Cl. In water-culture solutions with more than 2% NaCl all plants of *Aster* died within 1 month, while the best growth was made in 0.5% NaCl (Chapman). Exchangeable sodium in the same Norfolk marshes showed no significant annual drift and did not account for the total chloride except at 9 in. (22.5 cm.) depth.

III. Table 5 gives lists of salt-marsh species associated with *Aster* in various British localities. It will be seen from the arrangement in the table that *Aster* first appears in communities dominated by *Salicornia*, *Spartina stricta* or *Suaeda maritima* var. *flexilis*, and may assume dominance or co-dominance with *Glyceria maritima* in the next stage of succession. Thereafter it decreases in importance and becomes only an occasional plant in the General Salt Marsh Community, but increases somewhat in frequency in the Juncetum maritimi. It is most abundant on the east coast, plays a very subordinate role in those south coast localities where *Spartina Townsendii* dominates the lower marshes, and is nowhere very abundant in Scotland. It occurs with *Phragmites*, *Scirpus maritimus* and *S. Tabernaemontani*, *Phalaris*, *Juncus subnodulosus*, etc., in some east coast marshes where salinity is lowered by an influx of fresh water (Chapman, 1939).

The principal algal communities are very similar on most of the marshes. Those associated with abundant *Aster* are (a) sandy *Chlorophyceae* associates, (b) vernal *Ulothrix* consociates, (c) *Enteromorpha minima* consociates, (d) gelatinous *Cyanophyceae* associates, (e) autumn *Cyanophyceae* associates, (f) *Pelvetia-Bostrychia* associates, (g) *Bostrychia-Catenella* associates, (h) limicolous *Fucaceae* associates, (i) *Enteromorpha clathrata* f. *prostrata* associates (for complete lists see Chapman, 1939).

The associates of *Aster* on coastal marshes on the Continent are much as in Britain. An *Aster Tripolium* facies of inland salt meadows in Moravia includes *Aster Tripolium* var. *pannonicus* (Jacq.) Beck., *Atropis distans* Griseb., *Juncus Gerardi* Lois., *Melilotus dentata* Pers., *Lotus tenuifolius* Reichb., *Scorzonera humilis* Jacq., *Plantago maritima* L. *Aster* has also been reported from arable land in inland saline districts, where it is associated with *Chenopodium glaucum* L., *Delphinium Consolida* L., *Malva neglecta* Dalbr., *Lactuca saligna* L., *Dipsacus laciniatus* L., *Inula britannica* L., etc. (Hegi, 1906).

IV. Response to biotic factors. Dwarfed by grazing and perhaps reduced in density, but apparently not eliminated. The effects of grazing are most pronounced on some of the marshes of the west coast.

**Table 5.** Floristic composition of communities with *Aster Tripolium* as a constituent.

Also present *Scirpus maritimus* (l.c.d. in 11), *Carex extensa* (o. in 22), *Oenanthe Lachenalii* (o. in 22), *Samolus Valerandii* (o. in 23).

V. (a) *Gregariousness.* The mode of vegetative reproduction (see VI (a) below) causes the plant to grow in small patches in communities where it is abundant or dominant.

(b) *Performance.* The tallest plants are found where fresh water lowers the salinity or where there is abundant sewage. May reach 4 ft. (120 cm.) in height on muddy banks near sources of pollution, and Good & Waugh (1934) found plants 6 ft. (180 cm.) high on Redcliffe sands by the Humber. Flowers freely in all communities except the *Juncetum maritimi* and *Phragmitetum* where the plants are weak and spindly, presumably through reduced light supply. Grazing reduces flowering as well as height.

(c) *Effect of frost, drought, etc.* From its European distribution it is clear that *Aster* can endure prolonged and severe frost during the winter. For water relations see under II above.

VI. (a) (b) *Morphology.* The swollen, suberect rhizome, only  $\frac{1}{2}$ - $\frac{1}{2}$  in. (1.3-3.8 cm.) in length, with its apex close to the surface of the substratum, bears numerous adventitious roots extending to a depth of 6 in. to 1 ft. (15-30 cm.). The rhizome has numerous air spaces which are said by Iversen (1936) to be much better developed on wet marshy soils than on dry and well-aerated soils. The cortical cells have thick mucilaginous walls and some appear to be water-storing tracheids. Both rhizome and roots ultimately acquire a corky covering.

(c) *Mycorrhiza* has been reported (Mason, 1928).

(d) *Mode of perennation.* A semi-rosette hemicryptophyte. The leaves of next season remain just above the surface throughout the winter.

(e) *Vegetative reproduction.* Axillary buds on the rhizome form short 'offsets', and after 2 or 3 years the old rhizome begins to disintegrate, thus breaking the cluster into two or more separate parts. Buds in the axils of radical leaves are said to become detached and to function as vegetative propagules.

(f) *Longevity.* Perennial, but short-lived (see under VI (e) above).

(g) *Age of plant at first flowering.* Plants flower in their second year.

(h) *Frequency of setting viable seed.* Seed is set every year.

(i) *Ecotypes.* No information.

(j) *Chromosome number.*  $2n=18$  (Wulff, 1937; German material).

(k) *Physiological data.* Osmotic pressure of leaf sap = 26.8-32.1 atm. (Lundegårdh, 1919); % Cl in ash: leaves 41.3, stem 49.9, flowers 19.1.

VII. *Phenology.* (a) No information.

(b) New shoots appear in April or May.

(c) Flowers July to October. Var. *discoideus* Reichb. is said to flower in August and September. Early and late flowering types have been reported from the Continent.

(d) Fruits are dispersed from October onwards.

(e) Germinates from March onwards in any locality where the salinity is not too high.

VIII. (a) *Mode of pollination.* By insects. The hermaphrodite disk florets are protandrous, with the usual pollen-presentation mechanism. Self-pollination is possible (Knuth, 1908). The ray florets are female.

(b) *Insect visitors.* The following insects were recorded by Willis as visiting *Aster* on the south coast of Scotland (quoted by Knuth, 1908).

COLEOPTERA. Nitidulidae: *Meligethes aeneus* (Fab.), f., taking nectar and pollen.

DIPTERA. Muscidae: *Paregle [Anthomyia] radicum* (L.), f., and *Phaonia [Hyetodesia] incana* Wied.,\* both taking nectar and pollen; *Cryptolucilia [Lucilia] cornicina* (Fab.),\* f., taking nectar. Calliphoridae: *Onesia 'sepulchralis'* (Mg.),\* taking nectar. Cordyluridae: *Scatophaga stercoraria* (L.), f., taking nectar. Trypetidae: *Tephritis vespertina* Lw., taking nectar. Syrphidae: *Eristalis aeneus* (Scop.), f., *E. horticola* (Deg.), *E. tenax* (L.), f., *Platycheirus manicatus* (Mg.), all taking nectar.

HYMENOPTERA. Apidae: *Apis mellifera* L. [*mellifica* L.], *Bombus agrorum* (Fab.), *B. lapidarius* (L.), *B. pratorum* (L.), *B. terrestris* (L.), all taking nectar.

LEPIDOPTERA. Lycaenidae: *Lycaena [Polyommatus] phlaeas* (L.).

E. A. Woodruffe-Peacock (1923) records finding *Anthocoris nemorum* (L.) (HETEROPTERA: Anthocoridae) on flowers of *Aster Tripolium*, with pollen grains adhering to it.

(c) *Cleistogamous flowers* not known.

(d) *Apomixis*. No evidence from experiment.

(e) *Vivipary*. Not recorded.

(f) *Hybrids*. None recorded.

(g) *Amount of seed*. Average number of seeds per head = 18. The number of heads per plant ranges from about 25 in the first flowering season to as many as 90 in subsequent seasons, giving about 450 and about 1600 seeds per plant respectively.

(h) *Dispersal of fruits*. Principally by wind, but some must be carried by the tide to higher parts of the marsh. Fruits from one capitulum tend to stick together.

(i) *Viability*. Up to 90%.

(j) *Conditions for germination*. Percentage germination is decreased by concentration of NaCl above 1% (Chapman, Montfort & Brandrup, 1927):

*Percentage germination in NaCl solutions (Chapman)*

NaCl %	...	0	1	1·5	2	3	3·3	5	10
1933: tap water		45	25	—	10	—	0	0	0
1940: culture solution		90	29	11	6	0	—	—	—

(k) *Morphology of seedlings*. See Figs. 2 and 3. There is a circlet of root-hairs at the base of the hypocotyl, but root-hairs do not develop on the primary root until the fifth day of germination, and until then seedlings may be washed away by a flooding tide, so that periods of non-tidal exposure are important at this time. Cortical air-spaces can be detected in root and rhizome in the 1- and 5-day-old seedlings respectively. Adventitious roots appear about the 47th day.

(l) *Effective reproduction*. Both vegetatively and by seed.

IX. *Diseases. Parasites*. (a) The following list of insects exclusively attacking *Aster Tripolium* would probably be extended if close attention were paid to the plant. On the Continent a number of dipterous leaf-miners have been recorded some of which are sure to be found in this country.

HEMIPTERA-HOMOPTERA. Aphididae: *Macrosiphonella asteris* (Walk.); Essex, Kent. *Aphis tripolii* Laing; Essex.

DIPTERA. Trypetidae: *Paroxyna plantaginis* (Hal.); deforms the flower-heads.

LEPIDOPTERA. Tortricidae: *Phalonia affinitana* Dougl.; England to Lancs; larva first mines leaves and stem, later feeds in flower-heads. *Eucosma aemulana* Schläg.; Kent to

\* The specific identifications of the three species marked with an asterisk must be regarded as doubtful owing to changes in classification. *Onesia sepulchralis*, as now restricted, does not occur in Great Britain.

Dorset and Suffolk; larva feeds in flower-heads. *E. aspidiscana* Hb., larva of a variety of this species lives in the flower-heads. Coleophoridae: *Coleophora tripoliella* Hodgk.; Lancs; larva in case, feeding on seeds. Lyonetiidae: *Bucculatrix maritima* Staint.; England, eastern Ireland; larva mines leaves until nearly full-grown.

The following have been kind enough to answer inquiries about insect enemies of *Aster Tripolium*: Dr H. F. Barnes, Mr R. B. Benson, Mr W. E. China, Dr G. D. Morison.

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(b) The following fungi are confined to *Aster Tripolium* or are specially characteristic of it:

**BASIDIOMYCETES.** Uredinales: *Puccinia extensicola* Plow.; Norfolk; aecidal stage on *Aster*; alternate host is *Carex extensa*. *Puccinia Asteris*, Duby; (*P. Tripolii* Wallr.) Norfolk.

**ASCOMYCETES.** Pezizales: *Orbilia ulcerata* (Phill. & Plow.) Sacc. Hypocreales: *Gibberella cyanogena* (Desm.) Sacc.

**FUNGI IMPERFECTI.** Coelomycetes: *Phoma Tripolii* Died.; Anglesey. *Phomopsis Achilleae* von Höhn. f. *Asteris* Grove; Norfolk, Cornwall. *Rhabdospora nebulosa* Sacc. var. *minor* Desm.; Anglesey. *Lepiothyrium asterinum* B. & Br.; Norfolk, Suffolk, Lancs. Hyphomycetes: *Fusidium Asteris* Plow. & Phill. -*Ramularia Asteris* (Phill. & Plow.) Bubak.

(c) *Puccinia Asteris* Duby (*P. Tripolii* Wallr.) is the only serious disease. When present in abundance the leaves may be deformed. The incidence of this disease varies from year to year.

X. *History.* No information.

In preparing this account Dr Chapman obtained much detailed information from Mr Chater. Others who have very kindly offered data are: Prof. Sir W. Wright Smith; Prof. Walton; Prof. H. H. Dixon; Prof. Matthews; Mr Good; Dr Praeger; Mr Rilstone; whilst Mr Wilmott made constructive criticisms of the systematic portion.

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